ABSTRACT OF THESIS

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Title of Thesis Study of the Inheritance of Birthcoat

SUMMARY

The data from 15 month old ewe hoggets belonging to a flock of Welsh Mountain sheep under continuous selection for birthcoat type were analysed for correlated responses in fleece and fibre traits. Mass selection based on birthcoat type had been practised within two closed breeding groups: the High line, selected for hairy birthcoat (Type 6) and the Low Line selected for fibre birthcoat (Type 1). Selection on rams was intense, approximately 10%, but selection on females was light. This selection experiment has been in progress since 1953 at the Animal Breeding Research Organisation hill farm, Rhydyglafes, North Wales. The general farm conditions and management are fairly typical of those prevailing in the locality. Routine records for hoggets and mid-side fleece samples provided the material for this work.

The analysis of fleece measurements covered a period of 15 years (1953 to 1967) and their pooled overall mean values were as follows: fleece weight, 2.95 lb. (1877 observations). staple length, 9.76 cm. (1877 obs.) and dry wool weight per unit area of skin, 0.249 g/cm^2 (801 obs.). The annual differences between High and Low lines (Line differences) for these traits were small but significantly correlated with the corresponding line differences in cumulated section differentials of birthcoat type. Estimates of genetic correlations of various traits with birthcoat type (observed estimates) were calculated from regression of their line differences on the line differences for birthcoat selection differential. The observed genetic correlation estimates for fleece weight, staple length and dry wool weight were: 0.06, 0.12 and 0.12 respectively. Genetic correlation coefficients estimated by daughter-dam regression were in fairly good agreement with observed estimates; estimations by paternal half-sib analysis, however, gave negative correlation coefficients in each case.

Fleece samples from 50 unselected hoggets for 1953 and 142 hoggets showing effects of 6½ generations of selection for 1966, were used for analysis of fibre traits. Sub-samples of 100 - 120 fibres were separated into kempy, hairy and woolly fibres. Length, internal and external diameters, weight, medulla types and fibre densities were determined. The results indicated no significant line differences in samples for 1953 but significant differences in 1966 for all kempy fibre traits, virtually all hairy fibre traits and length and internal diameter of woolly fibres. Fleece composition line differences were significant only for 1966. The estimates for observed genetic correlations of fibre traits with birthcoat type were positive for all kempy and hairy fibre traits with the exception of length and weight of hairy fibres. In woolly fibres the only correlations with birthcoat type were in length and weight, these being positive and negative respectively.

British Wool Marketing Board (B.W.M.B.) fleece grades for High and Low Lines had shown clear differences in frequency distribution of fleece grades within lines since they were first recorded in 1958. Lines showed a consistent divergence in successive years; in 1967, good quality fleeces (Radnor types) predominated in the Low Line while a considerable increase of Low quality coloured fleeces was present in the High Line. Prices of fleece per pound and per hogget were negatively correlated with selection pressure for birthcoat type.

Use other side if necessary.

B.W.M.B. grades were found to be related to incidence of kemp and to staple length, and in general increases in these traits lead to deterioration of commercial quality.

In general all fleece and fibre traits showed correlated responses to selection for birthcoat type. Amongst fibre types kempy and hairy fibres indicated substantial changes while woolly fibres were less affected by selection. On the basis of these findings selection for hairy birthcoat type should lead to heavier fleeces, longer staples, heavier dry wool weight per unit area of skin, higher proportions of kempy and hairy fibres, larger and heavier kempy fibres, shorter and thicker hairy fibres and shorter and lighter woolly fibres.

STUDY OF THE INHERITANCE OF BIRTHCOAT

BY

J. C. CHIRGWIN B.

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I. INTRODUCTION

Variability and similarity are common features amongst group members of any species. Differences between individuals arise because organisms are complex systems which are made up of many parts, some of which may differ between group members; however, within species many of these parts will be the same in all individuals. The amount of differences and similarities which are found within a group is governed by the interplay of all component parts in each individual and it is this joint effect which introduces a balance between both features. This fact suggests that if important changes are introduced in a certain characteristic of an organism it would influence the entire system through a degree of disturbance of its inner balance; this could lead to a readjustment of all characteristics with changes not only in the initial characteristic but also in others.

Selection experiments provide a particular case where the balance of components becomes important. Selection for one or more traits in a closed population of individuals normally results in changes in the traits selected. In addition there are usually changes in other traits many of which may not be entirely predictable without a complete knowledge of the development of the individual. A study of these correlated changes requires reasonably large numbers of individuals bred over a number of generations. Selection experiments can be done fairly easily with laboratory animals because of their relatively low cost and short generation interval. Selection experiments in farm animals may take many years in giving some results but it is necessary to study these responses to selection in some detail because of the economic importance of the possible changes in overall performance.

Several selection experiments with farm animals have been started in the last 15 years or so, mostly with sheep, usually because of the lower cost of maintenance or shorter generation interval compared with pigs or cattle. Several such selection experiments are being run by the Animal Breeding Research Organisation. One of these experiments has been chosen as the experimental basis for this thesis. In this experiment Welsh Mountain sheep have been selected for birthcoat type at the Animal Breeding Research Organisation farm at Rhydyglafes in North Wales. Selection was started in 1952 and since then individual records and fleece samples have been collected. Data from adult sheep in this flock has been analysed by Purser (1967) who reported that selection for birthcoat had been effective and that correlated changes had occurred in bodyweight, fleece weight and fleece grades. These results and the accumulated information on individual performance for this flock suggested the possibility of a more detailed analysis of correlated changes in wool characteristics.

The present work is based on records and samples from yearling female sheep from Rhydyglafes' birthcoat selection experiment. This age group was chosen on account of two interesting features: firstly, because it is the earliest life stage to measure fleece production ability of future breeding ewes and secondly, because there are no complications arising from pregnancy and lactation.

The main purpose of the present work was to find out whether selection practised on lambs, with sole regard to birthcoat type, had had any influence on wool traits of yearling female sheep. The basic requirement was therefore to estimate genetic correlations between birthcoat type and wool characteristics, and to compare observed and expected estimates for these parameters.

The usefulness of genetic correlation estimates arises from the fact that the ultimate achievements of selection may depend on the type of genetic correlations present in the material. Nevertheless the accuracy in predicting correlated changes is usually restricted because these estimates commonly show large standard errors (Rae, 1952) and, in the case of selection experiments, because of the rapid changes that may occur in the genetic covariances between traits (Robertson, 1967). The material to be analysed here may introduce further limitations on the interpretation of genetic correlations on account of the amount of selection practised on the parents; in this data selection is intense only in the male side so that these limitations should be most important in methods involving relationship of offspring to the male parent.

II. LITERATURE REVIEW

References to reports appearing in the literature are to be presented under three main headings: first, those related to birthcoat, its description, systems of classification, inheritance and interrelations of this trait with productive characteristics; secondly, those reports which describe the genetic determination of fleece and body traits and their genetic associations; and finally, a brief comment on some selection experiments in sheep.

A. Birthcoat

Each fibre of the coat or fleece is produced by a follicle in the skin. These follicles may be classified into primary and secondary follicle types. The former are usually larger in size and each one has an associated muscle and a sebaceous gland. They can be subdivided into central primary follicles, which begin developing at about 60 days of foetal life, and lateral primary follicles which do so at about 70 days. The secondary follicles, in addition to anatomical differences, are the last to develop, initiation starting at about 80 to 90 days (Ryder and Stephenson, 1968). These follicle types show a basic pattern in their spatial arrangement on the skin: each central primary is associated with two laterals, one on each side, and a group of secondary follicles located between central and lateral follicles. (Carter, 1943).

Fibre formation also starts during foetal life so that at birth the body surface of lambs is covered by a protective coat. A striking feature of this birthcoat is the variation shown in the amount of coarse fibres, and this pecularity is readily noticeable between individual lambs (Ryder, 1965).

1. Fibre types

Birthcoat fibre types may show considerable morphological differences and these refer mainly to shape, thickness, incidence of medullation and fibre length. Several fibre types have been described in the literature (Duerden, 1927; Dry, 1933, 1934; Stephenson, 1956); among these, halo-hairs have received special attention from both sheep breeders and research workers.

Halo-hairs or birthcoat kemps come from primary follicles and are large, coarse fibres with a wire-like appearance and dull white colour. These fibres are stiff and springy to the touch though also showing poor elasticity and breaking fairly easily under tension.

The distribution and amount of halo-hairs in birthcoats present certain interesting relationships. Density or number of halo-hairs and body coverage appear to be interrelated so that increases in coverage over the body are also accompanied by increases in halo-hair density within body regions. Changes in density and in coverage show continuous gradation and within a particular coverage level there is a general trend for halo-hair density to increase from anterior to posterior regions while decreasing dorso-ventrally.

2. Classification systems

Halo-hairs are the most conspicuous of birthcoat fibre types and as lambs differ markedly in halo-hair incidence in particular body regions as well as in their spread over the body, these fibres have been used for birthcoat classification purposes.

White (1925) noted that the coat of Welsh lambs at birth could be classified into one of three main groups:

(a) Type 1. Thick hairy coat all over the body

(b) Type 2. Fine curling wool on the shoulders or fore part only, while a thick hairy coat is shown over the rest of the body

(c) Type 3. Fine curling wool all over except on the legs and tail.

Williams (1948) presented a five grade classification which had also been suggested by White. This classification system is basically the same with Type 1 and Type 3 as above but Type 2 is subdivided as follows:

(a) Type 2a. Thick hairy coat all over the body except for a slight reduction on the neck.

(b) Type 2. This grade shows a clear demarcation line at the heart girth, all fibres in front are short and fine while those behind form a thick hairy cover.

(c) Type 2c. Fine curly wool shows a clear predominance over the whole body with the exception of the hind quarters. It is usually possible to distinguish a faint demarcation line at the heart girth.

A six grade classification system is in use at Rhydyglafes (Purser and Karam, 1967), all grades being much the same as those presented by Williams but for a further subdivision of Williams' Type 2a grade into a Type 1b and Type 2a. The definition of the new grades are as follows:

(a) Type 1b. A dense hairy coat all over the body but with a slight reduction in halo hair density on the sides of the neck.

(b) Type 2a. A larger area of halo hair reduction in the fore part of the body with the exception of shoulders and sides. On the heart girth at the height of the elbow there is a marked reduction of halo hairs.

Fraser (1951) and Fraser and Short (1960) presented yet another classification system for birthcoat types, this one describing 12 groups. Individual grades are termed according to scale values from 1, for the extreme fine birthcoats, to 12, for the opposite extreme grade.

In order to indicate the similarities between the different classification systems reviewed above these are presented diagramatically in Table 1.

Table 1 . Birthcoat type classification systems

Body regions covered by halo-hairs	Authors			
	White (1925)	Williams (1948)	Purser and Karam (1967)	Fraser and Short (1960)
Thick, hairy fibres covering the whole body	1	1	1	12
			1b	11
		2a		
				10
			2a	9
Intermediate birthcoat grades	2	2	2	8
				7
				6
		2c	2c	5
				4
				3
Virtually no halo-hairs over the whole body	3	3	3	2
				1

3. Inheritance of birthcoat

Dry (1935) reported mating results among New Zealand Romney sheep which showed differences in halo-hair abundance and suggested that they supported a multifactorial interpretation. Mating results in Australian Merinos of known birthcoat types were analysed by Schinckel (1951) who tentatively proposed a monogenic interpretation. Similar mating results in Welsh Mountain sheep could not be accounted for by Schinckel's hypothesis but the results from this data provided some evidence for the presence of a dominant gene for extreme fine birthcoat (Rendel, 1954). Selection experiment results in Welsh Mountain sheep indicate that possibly only few loci control genetic variability of birthcoat (Purser, 1967); this is suggested by a decline of realised heritability estimates as selection proceeds.

Heritability estimates for birthcoat grade have been computed by several research workers and there seems to be good agreement in that its value is fairly high, ranging between 0.6 and 0.7. Table 2 presents a summary of some of the reported estimates. These values indicate that a fairly large proportion of the variance is additive genetic variance and therefore provide evidence that selection based on birthcoat type should be effective, and this has been verified in Welsh Mountain sheep (Purser, 1967).

Table 2 Birthcoat type heritability estimates

Breed	h^2	S.E.	Method	Authors
Welsh Mountain	0.60		O-P	Rendel, 1954
	0.65		Realised	Purser, 1967
Australian Merino	0.56		H-S	Morley, 1955
	0.80		O-P	Morley, 1955
	0.70	0.04	O-P	Schinckel, 1955
	0.70	0.08	F-S	Schinckel, 1955

Note: O-P stands for regression of offspring on parent
H-S stands for half-sib analysis
F-S stands for full-sib analysis

4. Associations between birthcoat and traits related to productive ability in sheep

The associations of birthcoat grade with other components of sheep production is to be presented by grouping them into: information from fibre analysis of adult fleeces, measurements of fleece traits and body weights, effects of birthcoat type on survival rates, and observations on sheep behaviour under bad weather conditions.

(a) Fibre characteristics.

Fibre characteristics of commercial fleeces have been reported by several research workers and those findings which are related to birthcoat type are briefly summarised below.

Results reported by Lockhart (1956) and Schinckel (1958) indicate that coarse birthcoats in Australian Merinos were associated with three main features of hogget fleeces: a higher variability in overall fibre diameter, an increased average difference between diameters of primary and secondary fibres, and higher values for diameters of primary fibres. These conclusions suggest that factors involved in the determination of birthcoat types mainly influence the activity of primary follicle fibres while showing no significant effects on secondary follicle fibres. A similar situation has been reported in New Zealand Romney sheep where N and nr genes show differential effects on follicle types; several research workers cited by Rae (1956) reported that crimp size, fibre length, percentage medullated fibres, percentage pigmented fibres and shedding percentage showed increases in primary follicle fibres from individuals carrying these genes, while no noticeable changes occurred in secondary follicles.

Fibre characteristics were also studied by Short (1951) and his analysis of Welsh Mountain fleeces underlined certain relationships between birthcoat grades and kempiness of commercial fleeces. The results presented in his study refer to several Welsh Mountain types and a group of Improved Welsh sheep. In terms of fleece quality, at one extreme was the Glamorgan type which is a heavily kemped mountain type, and at the other extreme was the Improved Welsh, a fine fleeced type. The main conclusions were as follows:

1. Hairy birthcoats occurred in all Glamorgan lambs while other Mountain types had only partial incidence, the remaining lambs within their flocks showing intermediate birthcoat types. Improved Welsh lambs showed birthcoats that ranged from intermediate to fine.
2. Sheep types also differed in the incidence of kemp in commercial fleeces, this incidence being classified into 4 main groups: 0 to 5%, 5 to 11%, 11 to 17% and 17 to 26%. Sheep types with low and intermediate kemp levels showed some degree of overlap but those with high incidence of kemp segregated clearly from the rest. Fleeces from Improved Welsh formed the majority of fleeces in the 0 to 4% group. Glamorgan fleeces were the only ones present in the 17 to 26% kemp group, while the other Mountain types contributed to both 5 to 11% and 11 to 17% groups.
3. Identical birthcoat classification of extremely hairy lambs for Glamorgan and for other Mountain types showed marked differences in kemp incidence for commercial fleeces; Glamorgan fleeces were <u>always</u> in the 17 to 26% group whereas the other Mountain types were <u>always</u> in the 11 to 17% group if their birthcoat type was hairy.

These results, considered as a whole, suggested to Short that the percentage of kemp in Welsh Mountain fleeces is genetically determined at four distinct, though slightly overlapping, levels of expression (Short, 1951).

Two considerations can be deduced from Short's fibre analysis: firstly, that sheep types have characteristic levels of expression for birthcoat type of lambs and for kempiness of adult fleeces, and secondly, that these two traits are related though not completely. In general the sheep types with high incidence of coarse birthcoats also present heavily kemped commercial fleeces while those with higher incidence of fine birthcoats were associated with low kemp incidence.

(b) Measurements of fleece traits and body weights.

Morley (1955) and Schinckel (1958) studied fleece characteristics and body weights in Australian Merino yearlings relating these traits to their birthcoat grades, and a similar analysis was reported for Welsh Mountain sheep by Purser and Karam (1967). The report on Welsh Mountain included information on carcass characteristics and pre-slaughter weight at approximately 200 days of age; in this work corrections were introduced to standardise the data so that the correlations presented are partial correlations. Wilson _et al_ (1962) working with data from Rambouillet, Targhee and Columbia lambs studied several adult wool traits and body weight with relation to birthcoat type. Several estimates of phenotypic correlations with birthcoat appear in Table 3b.

Table Fleece and body traits associated with birthcoat grade

Trait	Values associated with coarse birthcoat grade	r_p	Authors	
No. of crimps per inch	Fewer crimps	-0.13**	Morley,	1955
	" "	-0.28**	Schinckel,	1958
Staple length	No association	0.00	Morley,	1955
	" "	-	Schinckel,	1953
		0.04	Wilson,	1962
Greasy fleece weight	Higher weight	0.15**	Morley,	1955
	No association	-	Schinckel,	1958
	No association	0.05	Wilson,	1962
	No association	-0.05	Purser _et al_,	1967
Clean fleece fleece weight	Higher weight	0.16**	Morley,	1955
	No association	-	Schinckel,	1958
	No association	0.08	Wilson,	1962
Body weights:				
From birth to 18 months	No association	-0.01 to 0.09	Purser, _et al_	1967
	No association	-0.03 to -0.06	Wilson,	1962
Yearling weight	No association	0.05	Morley,	1955
	" "	-	Schinckel,	1958
	" "	- 0.03	Wilson,	1962
Pre-slaughter	No association	0.05	Purser, _et al_	1967
Carcass weight	Lighter weight	- 0.13*	Purser, _et al_	1967
Dressing %	Lower percentage	- 0.11*	Purser, _et al_	1967

Note: r_p stands for phenotypic correlation with birthcoat grade

* $P < 0.05$

** $P < 0.01$

Number of crimps per inch was the only trait that gave consistent and significant phenotypic correlations with birthcoat grade while data for staple length provided no evidence of any association between these traits; however, Morley (1955) reported a value of 0.15 for a non significant genetic correlation between birthcoat and staple length.

Greasy fleece weight and clean fleece weight showed similar results and highly significant phenotypic correlations with birthcoat type occurred only in Morley's data while no association was present in either Schinckel or Purser and Karam's analysis. Morley (1955) using a parent-offspring regression calculated highly significant genetic correlations for both fleece weights, their respective values being: 0.24 and 0.26 respectively, while similar estimates for Welsh Mountain sheep showed greasy fleece to be negatively correlated to birthcoat grade; values for the latter analysis were: -0.40 from a half sib analysis and -0.28 from a daughter-dam regression (Purser and Karam, 1967).

Birthcoat grade and body weights presented no phenotypic correlations in any of the reviewed reports. A genetic correlation with a value of 0.25 was found between birthcoat grade and body weight at 10 months of age, and a value of 0.12 was reported for a similar correlation with yearling weight (Morley, 1955); the former estimate was calculated by half-sib analysis while the latter was obtained by parent-offspring regression. Purser and Karam (1967) presented an estimate of -0.16 for the genetic correlation between birthcoat and birthweight but correlation with weights at later ages were all positive and steadily increasing with age from: 0.09 at 3 months to 0.36 at 18 months of age.

Pre-slaughter weights at approximately 200 days of age showed no phenotypic correlation with birthcoat grade but carcass weight and dressing-out percentages gave significant negative correlations.

(c) Survival rates

Davies (1964) reported that mortality rates among Australian Merino lambs showed no obvious trend with birthcoat type; figures for fine, medium and hairy types were 16.2%, 18.9% and 17.6%, respectively. Mullaney (1966), analysing data from Australian Merino, Corriedale and Polwarth lambs, found no significant difference in survival until 20 days among groups with different birthcoat types; however, in a particularly severe year lambs with coarser birthcoats did seem to survive better.

Survival rate among Welsh Mountain lambs was related to birthcoat type by Purser and Karam (1967) and their results indicate that, in general, of the six birthcoat type groups those lambs with intermediate birthcoats survived better up to weaning. Extremely fine coated lambs showed the highest mortality rate, about 16%, followed by those with extremely hairy birthcoats which showed a figure of approximately 9%, while "birthcoat type 4" lambs had the best survival with a mortality of only 4%. Intermediate birthcoat types had a mortality range from approximately 4% to 10%.

(d) Sheep behaviour under bad weather conditions

Welsh mountain sheep with different fleece types were observed by Short (1951) under bad weather conditions. His observations on adult sheep indicate that wool length, staple formation and type of tip are critical factors in the wetting and drying processes of the fleece. Under prolonged heavy rain, sheep with close, short fleeces were reported to resist slightly longer to initial wetting than sheep with longer, more open and well stapled fleeces; however, penetration was less complete in well stapled sheep and vigorous shaking enabled them to throw off surplus water. Shaking was far less effective in removing water from close fleeced sheep.

Results for lambs were similar to those mentioned for adult sheep and the age of the lambs under observation was approximately 3 months. Under heavy rain fine coated lambs resited penetration for a longer initial period, 15 to 20 minutes compared to 10 to 15 minutes for the more open fleeced lambs; however, once water reached skin level the latter lambs shook off much of the free water while the former became thoroughly soaked.

Thermoregulation aspects of the new born Australian Merino lambs were related to birthcoat type by Alexander (1961). The amount of heat produced by lambs as a response to cold was considerably lower in lambs with hairy birthcoats then in those with fine birthcoats; this indicates that lambs with hairy coats are able to conserve heat more readily than fine coated lambs.

Judging by the results presented above differences in coat characteristics seem to influence the wetting and drying processes of lambs and adult sheep, and this is possibly associated with differential demands on heat production.

(e) Conclusions on birthcoat type associations with productive traits

All factors associated with birthcoat grade and which were reviewed above modify production characteristics in some way or another. Hill sheep are influenced by many factors and their production levels are greatly modified by environmental conditions. White (1925) and Doney (1955) have commented that as sheep products from mountain breeds are brought forth under rigorous hill conditions, any breeding programme must pay due consideration to aspects related to hardiness. A definition for this term was proposed by Doney (1955) as "the degree of adaptation required to give maximum long term production within the normal variation of the prevailing environment". He suggested also that body size developed under hill conditions was a good measure of both individual adaptability and economic value; September weight was reported by Doney (1955) as the best single guide to measure hardiness as defined above, and this weight corresponded to weaning weight at 20 to 25 weeks of age.

Hardiness as regarded in Doney's classification is a trait which is made up of many component parts and the evidence summarised under the different headings of this section seem to indicate that several factors associated with birthcoat grade can possibly modify one or more of these components.

B. Productive Traits in Sheep

Body weight and fleece weight in sheep are among the more important economic traits and numerous studies include reports on these characteristics at different ages and in different breeds. Estimates of parameters such as heritabilities and phenotypic correlations are commonly found in the literature but genetic correlations appear in a far more limited scale.

1. Heritability

Reported heritability estimates for productive traits in sheep present a wide range of values and it is difficult to generalise on the degree of heritability shown by a certain trait; the range of the more frequently reported estimates may serve as an approximation to this generalisation.

Greasy fleece weight shows numerous reports of heritability estimates and most of them lie between 0.30 and 0.50; estimates reported by several research workers appear in Table 4 . Noteable exceptions to the common range are values calculated for New Zealand Romney and Tsigai breeds, which are lower: 0.10 to 0.15, and those for Welsh Mountain: 0.60, which are higher.

Table 4 Heritability estimates for yearling greasy fleece weight

Breeds	h^2	S.E.	Methods	Authors
Tsigai	0.11		D-D	Zelnik *et al*, 1964
N.Z. Romney	0.10 to 0.15		O-D	McMahon, 1943
	0.17		D-D	Rae, 1950
Corriedale	0.72		D-D	Rasmussen, 1942
	0.52		D-D	Wright *et al*, 1953
	0.35		O-D	Katada *et al*, 1962
Rambouillet	0.28		O-D	Terril *et al*, 1943
	0.66		H-S	Shelton *et al*, 1953
S. African Merino	0.09	0.09	H-S	Bosman, 1958
	0.47	0.06	H-S	Bosman, 1958
Australian Merino	0.39	0.10	O-P	Morley, 1951
	0.44		H-S	Morley, 1955
	0.40	0.06	O-P	Morley, 1955
	0.45	0.06	H-S	Young *et al*, 1965
	0.45	0.12	O-D	Pattie, 1965
	0.75	0.15	H-S	Pattie, 1965
Welsh Mountain	0.58	0.11	O-D	Dalton, 1952
	0.61	0.11	D-Dr	Doney, 1958

Note: D-D stands for daughter-dam regression analysis
D-Dr stands for daughter-dam correlation analysis
O-D stands for offspring-dam regression analysis
H-S stands for half-sib analysis

Heritability estimates for clean fleece weight are on the whole much like those for greasy fleece weight but somewhat higher; most estimates lie between 0.40 and 0.60. Reported estimates appear below in Table 5.

Table 5 Heritability estimates for yearling clean fleece weight

Breeds	h^2	S.E.	Methods	Authors	
Rambouillet	0.38		O-D	Terrill *et al*,	1943
	0.61		H-S	Shelton *et al*,	1954
Romnelet	0.4'	0.08	D-D	Veseley *et al*,	1961
S. African Merino	0.23	0.13	H-S	Bosman,	1958
	0.44	0.13	H-S	Bosman,	1958
Australian Merino	0.62	0.27	O-P	Morley,	1950
	0.26		H-S	Morley,	1955
	0.47	0.07	O-P	Morley,	1955
	0.45	0.06	H-S	Young *et al*,	1960
	0.34	0.09	D-Dr	Beattie,	1962
	0.40	0.11	O-D	Pattie,	1965
	0.76	0.15	H-S	Pattie,	1965

The range of values reported for heritability estimates of staple length is wide, most of them falling between 0.30 and 0.60. Table 6 presents some staple length heritability estimates.

Table 6 Heritability estimates for yearling staple length

Breeds	h^2	S.E.	Methods	Authors	
N.Z. Romney	0.35	0.07	D-D	Rae,	1950
Corriedale	0.37		O-D	Katada _et al_,	1962
Rambouillet	0.36		O-D	Terrill _et al_,	1943
	0.67		H-S	Shelton, _et al_,	1954
Australian Merino	0.22	0.22	O-P	Morley,	1950
	0.52		H-S	Morley,	1955
	0.56	0.07	O-P	Morley,	1955
	0.37	0.06	H-S	Young _et al_,	1960
	0.50	0.09	D-Dr	Beattie,	1962
	0.38	0.11	O-D	Pattie,	1965
	0.62	0.15	H-S	Pattie,	1965
Welsh Mountain	0.73	0.14	O-Dr	Doney,	1958

Published reports provide relatively fewer estimates for fibre diameter than for other fleece characteristics, and these indicate that most values fall in a wide range, between 0.30 and 0.60. Reported estimates appear below in Table 7 .

Table 7 Heritability estimates for yearling fibre diameter

Breeds	h^2	S.E.	Methods	Authors	
Rambouillet	0.57		H-S	Shelton *et al*,	1954
S. African Merino	0.29	0.09	H-S	Bosman,	1958
	0.34	0.12	H-S	Bosman,	1958
Australian Merino	0.45	0.06	H-S	Young *et al*,	1960
	0.57	0.08	D-Dr	Beattie,	1962

Birthweight estimates of heritability are less variable than those reported for most body weight and fleece characteristics. Actual values range from 0.10 to 0.40 while the most commonly reported estimates fall between 0.20 and 0.35. In Table 8 below, some estimates for birthweight heritability are presented.

Table 8 Birthweight heritability estimates

Breeds	h^2	S.E.	Method	Authors	
Shropshire	0.08		O-D	Esminger *et al*,	1943
	0.10				
Hampshire	0.20		O-D	Esminger *et al*,	1943
	0.30			Chapman *et al*,	1932
Southdown	0.34		H-S	Esminger *et al*,	1943
	0.40				
Dala and Steiger	0.12	0.05	H-S	Gjendrem,	1967
Rahmani	0.16		H-S	Karam,	1959
Ossimi	0.34		O-D	Ragab *et al*,	1953
Mutton Merino	0.22			Jakubec,	1964
	0.34				
Australian Merino	0.31	0.10	H-S	Dun *et al*,	1965
Welsh Mountain	0.21	0.07	D-D	Dalton,	1962
Welsh Mountain	0.39	0.16	D-Dr	Doney,	1955

As a contrast to birthweight estimates those of weaning weight are more variable, actual values ranging from 0.05 to 0.80 but the more usual estimates falling between 0.10 and 0.30. Figures for estimates on Welsh Mountain data around 0.60, show consistently higher values, than the range of commonly reported estimates. Some reported estimates appear below in Table 9 .

Table 9 Weaning weight heritability estimates

Breeds	h^2	S.E.	Methods	Authors	
Southdown	0.04 0.06		D-D	Ensminger *et al*,	1943
Shropshire	0.08 0.12		D-D	Ensminger *et al*,	1943
Dala and Steiger	0.18	0.06	H-S	Gjendrem,	1967
Rahmani	0.18		H-S	Karam,	1959
Ossimi	0.10 0.29		D-D	Ragab *et al*,	1953
Targhee	0.00 0.08		D-D	Hazel *et al*,	1945
Rambouillet	0.30		D-D	Hazel *et al*,	1945
Australian Merino	0.10	0.04	O-D	Young *et al*,	1965
Mutton Merino	0.19 0.77			Jakubec,	1964
Australian Merino ♂	0.32	0.10	O-D	Pattie,	1965
Australian Merino ♂	0.19	0.14	H-S	Pattie,	1965
Australian Merino ♀	0.28	0.10	O-D	Pattie,	1965
Australian Merino ♀	0.18	0.07	H-S	Pattie,	1965
Australian Merino ♀	0.31	0.05	Realised	Pattie,	1965
Australian Merino ♂	0.19	0.07	Realised	Pattie,	1965
Welsh Mountain	0.51	0.07	D-D	Dalton,	1963
Welsh Mountain	0.68	0.06	D-Dr	Doney,	1958

The more usual figures reported for yearling body weight give a slightly larger range than birthweight estimates and most values fall between 0.20 and 0.40. Welsh Mountain estimates are again an exception with values of approximately 0.60. Table 10 summarises some of the reported estimates for yearling weight heritability.

Table 10 Heritability estimates for yearling bodyweight

Breeds	h^2	S.E.	Methods	Authors	
Rahmani	0.19		H-S	Karam,	1959
Romnelet	0.37	0.11	D-D	Veseley et al,	1961
Rambouillet	0.40		D-D	Terrill et al,	1943
Corriedale	0.41*		O-D	Katada et al,	1962 (1)
Corriedale	0.55**		O-D	Katada et al,	1962 (2)
Mutton Merino	0.21		H-S	Jakubec,	1964
S. African Merino	0.42	0.13	H-S	Bosman,	1958
	0.54	0.11	H-S	Bosman,	1958
Australian Merino	0.36	0.23	O-P	Morley,	1951 (3)
	0.09		H-S	Morley,	1955
	0.36	0.08	O-P	Morley,	1955
	0.47	0.12	O-D	Pattie,	1965
	0.40	0.11	H-S	Pattie,	1965
Welsh Mountain	0.59	0.11	D-Dr	Doney,	1958

Note: (1) Body weight measured before shearing
(2) Body weight measured after shearing
(3) Body weight at 10 months of age

* $P < 0.05$ ** $P < 0.01$

Heritability estimates given in the above tables show that the amount of additive genetic variance for fleece traits are generally at levels of 0.30 to 0.50 and that estimates for fleece weights are less variable than those for staple length and fibre diameter. Estimates of bodyweight heritability are commonly found to lie between 0.20 and 0.40 but weaning weight estimates are more variable than the rest and generally tend to slightly lower values: 0.10 to 0.30. The main conclusion behind these figures relates to the expected responses to selection; data for these estimates come from many breeds and environments so that it can be concluded that, in general, there is sufficient additive genetic variance present in these traits for selection to be effective. Correlated responses however, are governed by the heritability of selected and unselected traits and by their respective genetic correlations. Heritability levels for birthcoat type, fleece traits, fibre diameter and body weights seem large enough not to be the limiting factors of correlated changes. Correlations between birthcoat type and other traits will be presented in the next section.

2. Phenotypic correlations

Estimates for these parameters have been reported by several research workers and include information from many breeds. Some of these estimates are presented in Table 12b and they come mainly from studies on Australian Merino sheep.

Values for correlations will be assessed using Turner's classification for different magnitudes (Turner, 1964) viz:

(a) High values: equal or greater than 0.60

(b) Medium values: equal to 0.40 or less than 0.60

(c) Low values: equal to 0.20 or less than 0.40

(d) Negligible values: less than 0.20

Correlations between fleece and body traits with greasy and clean fleece weights indicated similar values for these parameters but with a slight trend towards higher values in the latter. On account of this similarity in their estimates and the generally high correlation found between greasy and clean fleece weights the correlations tabulated in Table 12b refer mainly to greasy fleece weight.

From the figures presented in Table 11 it can be concluded that in general positive phenotypic correlations, ranging from negligible to medium values, are to be found among fleece weight, staple length and yearling weight. The same conclusion applies to correlations among fibre diameter, fleece weight and yearling bodyweight. All traits, save yearling bodyweight, seemed negatively correlated to crimps per inch but values were low; staple length and fibre diameter also showed similar results.

Table II Phenotypic correlations between fleece traits and bodyweight

Traits	Breeds	Greasy fleece	Staple length	Fibre diam.	Crimps per inch	Yearling body weight	Authors	
Clean fleece weight	Rambouillet	0.72	0.55	-	-	-	Terrill *et al*,	1950
	S. African Merino	0.85	-	0.34	-0.27	0.69	Bosman,	1958
		0.86	-	0.44	-0.20	0.66	Bosman,	1958
	Australian Merino	0.77	0.48	0.14	-0.36	0.25	Morley,	1951
		-	0.30	0.44	-	-	Shelton *et al*,	1954
		-	0.39	-	-0.32	0.37	Morley,	1955
		-	0.49	0.05	-0.45	0.13	Beattie,	1962 (1)
Greasy fleece weight	Welsh Mountain		0.28	-	-	-	Doney,	1958
	N.Z. Romney	-	0.45	-	-	-	Rae,	1950
	S. African Merino	-	-	-	-	0.20	Bosman,	1958
		-	-	-	-	0.16	Bosman,	1958
	Australian Merino	-	0.22	0.15	-0.25	0.30	Morley,	1951
		-	0.11	0.30	-	-	Shelton *et al*,	1954
		-	0.30	-	-0.21	0.30	Morley,	1955
		-	0.39	0.06	-0.33	0.15	Beattie,	1962 (1)
	Spanish Merino	-	0.27	-	-	0.15	Shanchez Belda,	1950 (1)
Staple length	Rambouillet	-	-	-0.19	-	-	Jones *et al*,	1944
	Australian Merino	-	-	0.03	-0.34	0.12	Morley,	1951
		-	-	-0.26	-	-	Shelton *et al*,	1954
		-	-	-	-0.22	0.10	Morley,	1955
		-	-	-	-0.36	0.05	Beattie,	1962 (1)
Fibre diam.	Australian Merino	-	-	-	-0.21	0.11	Beattie,	1962 (1)
Crimps per inch	Australian Merino	-	-	-	-	0.15	Morley,	1951
		-	-	-	-	0.05	Morley,	1955
		-	-	-	-	0.00	Beattie,	1962 (1)

Note: (1) refers to adult bodyweight

3. Genetic correlations

Some of the estimates of genetic correlations which appear in the literature are presented in Table 12 . These estimates were derived from yearling sheep in the case of the estimates presented by Morley (1955) for Australian Merinos and by Rae (1950) for New Zealand Romney. Estimates calculated by Doney (1958) refer to adult Welsh Mountain sheep and the same applies to those reported by Beattie (1962) who worked with adult Australian Merinos.

Table 12 Estimates of genetic correlations between fleece and body characteristics

Traits	Staple length	Crimps per inch	Method	Authors
Clean fleece weight	0.39**	0.53**	O-P	Morley, 1955
	0.89 ± 0.16	-0.96 ± 0.19	D-D	Beattie, 1962
Greasy fleece weight	0.02	-0.56**	O-P	Morley, 1955
	0.70 ± 0.17	-0.87 ± 0.20	D-D	Beattie, 1962
	0.83	-	D-Dr	Doney, 1958
Staple length	-	-0.34**	O-P	Morley, 1955
	-	-0.75 ± 0.12	D-D	Beattie, 1962
Count	0.73 ± 0.16	-	D-D	Rae, 1950
Hairiness	0.41 ± 0.12	-	D-D	Rae, 1950

Note: * $P < 0.05$
** $P < 0.01$

Estimates in Table 12 indicate that clean and greasy fleece weights showed similar correlations with staple length and crimps per inch; furthermore a significant genetic correlation of: 0.65 was reported by Morley (1955) between these two fleece weights. Turner (1964) indicated that these two traits showed a high, positive correlation.

Correlation values presented in Table 12b indicate positive correlations between fleece weight and staple length but negative estimates for those between crimps per inch with fleece weight and staple length; the one exception was a negative estimate between greasy fleece weight and staple length reported by Morley (1955) but its magnitude was negligible: -0.02. Turner (1964) reported that in Australian Merino sheep measurements on individuals within a flock gave positive correlations of medium magnitude between clean fleece weight and staple length. Negative correlations between clean fleece weight and crimps per inch were also reported by the same author but Peppin flocks gave medium to high values while strong wool flocks showed low estimates for this genetic correlation. Crimps per inch and staple length were also negatively correlated in data analysed by Turner (1964) and estimates ranged from medium to high values. Crimps per inch were also reported to be negatively correlated to fibre diameter but magnitudes were low (Turner, 1964).

Staple length showed positive genetic correlations with commercial fleece quality traits in New Zealand Romney sheep. Longer staples were associated with higher quality number or count and with greater hairiness, (Rae, 1950).

On the whole these results for genetic correlation estimates are similar to those presented for phenotypic correlations but values are generally higher. This information on genetic correlations also suggests that continued selection for certain fleece traits is expected to bring about changes in other unselected fleece traits. From a practical point of view the most important of these correlations seems to be that between fleece weight and traits related to fleece quality (Rae, 1952).

Table 13 Estimates of genetic correlations between body and fleece traits

Traits	Weaning weight	Method	Authors
Greasy fleece weight	0.43	D-Dr	Doney, 1958
	0.06 ± 0.22	O-D	Pattie, 1965
	0.48 ± 0.22	H-S	Pattie, 1965
	0.08	Realised	Pattie, 1965
Staple length	0.39	D-Dr	Doney, 1958
	-0.15 ± 0.23	O-D	Pattie, 1965
	0.46 ± 0.21	H-S	Pattie, 1965
	0.17	Realised	Pattie, 1965
Skin folds	-0.34**	O-P	Morley, 1954
	-0.74 ± 0.12	O-D	Pattie, 1965
	0.08 ± 0.53	H-S	Pattie, 1965
	-1.46	Realised	Pattie, 1965
Birth weight	0.50	D-Dr	Doney, 1958
	0.73 ± 0.26	H-S	Vogt _et al_, 1967

Several estimates for genetic correlations between body weight and other traits are presented in Table 13.

In general positive genetic correlations have been reported for weaning weight with fleece weight, staple length and birthweight, the only exception being a non-significant estimate of: -0.15 between weaning weight and staple length (Pattie, 1965). However, Morley (1955) also reported a negative correlation of: -0.26 between yearling bodyweight and staple length, and this value was significant at the 5% probability level. Turner (1964) indicates that bodyweight and staple length in Merino show a negative association of low magnitude in Peppin flocks while no association is present in strong wool flocks. The genetic correlation estimates given in Table 13 suggest that weaning weight and the incidence of skin folds are negatively associated.

The general conclusion to be drawn from these correlations between bodyweight and other traits is similar to that mentioned for fleece traits: it appears that continued selection for bodyweight could cause correlated changes in some fleece traits and visa-versa.

The estimates presented in this section illustrate the fact that fleece and body traits may share sources of genetic variability so that selection for a certain trait may cause changes in unselected traits. However, genetic correlations may differ quite markedly even amongst flocks of the same breed so that their usefulness to predict correlated changes is limited.

C. Selection Experiments

Reports of several selection experiments in sheep provide evidence of direct and correlated responses to selection under diverse environmental conditions and in different breeds. A brief description of some of these experiments is given below to illustrate the long-term effect of selection on sheep populations.

Four long-term two-way selection experiments in hill sheep were reported by Purser (1967), one based on birthcoat type in Welsh Mountain sheep and two in Scottish Blackface, which had degree of fibre medullation and cannon-bone length as their respective selection criteria. All three experiments responded to selection in good agreement with expected rates of change for each trait and, in all cases, evidence was obtained for correlated responses.

Selection for birthcoat induced changes in bodyweight, fleece weight, fleece quality and lamb survival. Hairier birthcoats were associated with lower birthweights but higher weights at weaning and at adult stages. Fine birthcoats gave higher fleece weights and fleeces of better quality. Intermediate birthcoats showed a substantial lamb survival advantage over both extreme birthcoat types.

Correlated changes have occurred in fleece characteristics and in liveweights due to selection for medullation index at eight weeks of age. Fleeces in the low medullation line were lighter and had greater amount of kemps from 4 months of age onwards than those for the high medullation line.

Selection for higher medullation was associated with lower weaning weights but adult size remained unchanged.

Sheep selected for cannon-bone length showed correlated changes in body shape and those selected for short cannon-bone length became wider across the shoulders and pelvis, and also stopped growing at an earlier age.

Australian Merinos were selected for high clean wool weight at Cunnamulla, Queensland, and response to selection was assessed by comparison of the selected lines with a random control group (Turner, 1968). Results for the period 1950-1959 indicate significant response in high clean wool weight while significant correlated responses occurred in greasy fleece weight, clean yield and number of fibres per square millimeter, all of which showed positive and consistent trend in their changes. Bodyweight and staple length also presented positive and consistent changes but responses were generally non-significant. Pattie (1965) reported a two-way selection experiment based on weaning weight conducted in Australian Merinos at Trangie, New South Wales; response was measured by differences between the selection lines and a control group. The experiment was begun in 1951 and results for the period 1951-1961 indicate a consistent divergence between selection lines; after four generations of selection the High-Low weaning weight difference for 1961 indicated a superiority of approximately 30% to the High line. Estimates of realised heritability based on direct response and on the amount of selection applied to these lines agreed well with heritability estimates computed from the control group by dam-offspring and half-sib analysis; these estimates were: 0.25 and 0.24 respectively. Correlated changes occurred in

17 month bodyweight and yearling fleece weight but on account of a stronger genetic correlation changes were greater in the former trait.

Experiments based on fertility as selection criteria were reported by Wallace (1964) from a flock of New Zealand Romneys kept at Ruakura; the experimental flock was initiated in 1948 and consisted of a high, a low and a control line. After the initiation of the experiment animals in the selection lines have been chosen with regard to their dam's lambing performance while no attention has been paid to it in the control group. Selection results indicate a substantial response in the high fertility line; during the first four years this line averaged only 1% higher than the total flock in lambing percentage but between 1960-1963 the corresponding figure was 26%. Performance results for the low fertility line were consistently similar to those of the control group. Body weights and fleece weights showed changes during the selection period: higher weaning weights were found for both single and twin lambs in the High fertility line but fleece weights for the 1960-63 period presented a greater drop in this line than in any other group. Fleece weight and body weights of ewes at tupping steadily decreased in all lines and the causes of these changes are as yet not properly understood.

Australian Merinos were selected for reproductive rate at Deniliquin, Queensland; response to selection was measured as the divergence between selection lines by means of a two-way selection experiment (Turner, 1962). Selection was applied only to males and within each selection line rams were chosen on the lambing percentage of their dams and grand-dams. In 1958 when the experiment was initiated ewes were distributed into the high and low performance lines according to their previous lambing records but no subsequent selection was practiced in the female side. As a consequence of the initial distribution of ewes, selection lines differed in 1958 in their lambing percentages, High Twinning line performance exceeding that of the Low Twinning line by 12%. From 1958 to 1963 lines diverged steadily, at a rate of approximately 3% per year, indicating that selection for twinning rate was effective.

As a general conclusion from the selection experiments described above it can be inferred that their results are in good agreement with theoretical expectations and provide evidence on the effectiveness of selection when based on single traits with reasonably high heritability. These results also indicate that populations under intense and continued selection are likely to change in characteristics which although not under selection themselves are modified on account of a genetic correlation with the selected trait.

III. RHYDYGLAFES' SELECTION EXPERIMENT

There are several problems that can be studied by performing selection experiments. Information from selection experiments in farm animals is helpful for it can provide estimates of genetic parameters and give indications on their possible changes under selection. In addition, comparisons between expected and observed results show the amount of agreement between theoretical calculations based on a series of assumptions and empirical results; these comparisons are applicable to both direct and correlated responses. Successful selection experiments may lead after some time to the formation of groups that are genetically different for a number of traits but which derived from a common base population; such groups are suitable material for studies on the biology of different traits. Information on problems such as those outlined above can lead to a better understanding of performance ability in farm animals and of the ways to modify its expression.

Selection experiments in farm animals, as distinct from practical improvement programmes, may be based on traits which are associated in some degree to economically valuable characters but the traits should be chosen to ensure that results occur within a reasonable period of time. Birthcoat type is the selection criteria in one of the Animal Breeding Research Organisation (A.B.R.O.) selection experiments. The main advantages of using this trait is its early expression which allows a high selection intensity and a short generation interval.

This experiment provides the basic material for the study reported here, the brief description of the experiment which follows is derived from A.B.R.O.'s unpublished annual reports.

A. Materials

Since 1952 the Animal Breeding Research Organisation has conducted a selection experiment at Rhydyglafes farm, Merionethshire, North Wales, and using for that purpose a flock of Welsh Mountain sheep. The conditions at Rhydyglafes can be considered to be typical of local Welsh hill farms. They are dedicated mainly to sheep production and characterised by having some lowland wintering ground though their main grazing areas are at altitudes of 1200 to 2400 feet.

Climatic conditions at Rhydyglafes can be roughly divided into two periods: one of them which lasts for some 7 to 8 months from September-October to March-May, having heavy monthly rainfall (5.4" on average), with high incidence of morning frost (on average 12 to 20 days per month) and showing the lowest averages for maximum and minimum daily temperatures (57°F and 19°F respectively); the remaining months show a considerable improvement with a reduction by half in rainfall (2.8" on average), a substantial raise in daily temperatures (73°F for maximum temperatures and 30°F for minimum temperatures) and generally with no frost from June till August. A summary of monthly averages for some climatic factors are presented in Table 14; this information was taken from A.B.R.O.'s annual reports and covering the period 1959 to 1966.

Table 14 Monthly averages of some climatic factors at Rhydyglafes

Factors	Months											
	1	2	3	4	5	6	7	8	9	10	11	12
Rainfall, in./month	5.2	2.6	2.1	3.5	2.5	1.7	2.9	2.8	3.3	4.1	4.7	7.5
Max. Temp., °F, daily ave.	53	57	59	63	70	76	75	73	75	68	57	55
Min. Temp., °F, daily ave.	13	22	21	27	28	32	34	36	30	28	21	15
No. of days with rain	20	19	15	18	16	15	17	19	17	18	22	22
No. of days with air frost	17	13	12	7	1	-	-		-	5	12	12
No. of days with ground frost	23	15	19	11	4	-	-	1	1	10	17	21

The number of sheep under selection for birthcoat type is a flock of approximately 400 ewes and these are distributed into three age groups; the ewes lamb for their first time at about 2 years of age and they produce two more lamb crops before being drafted.

Tupping generally takes place between late October to late November and ewes are brought down from the mountain at this time for mating. Ewes graze on high ground during most of the year but during winter they are brought down around January and kept in fields at altitudes of approximately 1100 feet. Lambing spreads from late March to mid-April and most ewes lamb in exposed and unfavourable conditions. In early May the flock is gradually taken back to the hill grounds, the ewes with the older lambs going first. Ewes rearing twins remain in the low grounds. Before taking the flock to the mountain female lambs are docked, surplus males castrated and routine health measures are performed. Sheep are sheared early July and it is usual to wash them in mountain streams before this operation. Weaning starts after this gathering and by mid-August all lambs are weaned. After weaning draft ewes are selected and subsequently disposed of, generally during September. Wether lambs are usually marketed between October and November.

B. Experimental Procedure

Experimental needs impose additional work over and above the normal management routine and these requirements refer to recordings, special classification and measurements, controlled matings and other procedures.

1. Records

Since the initiation of the selection experiment in 1952 detailed records are available for individuals born to both selection lines; partial information on past performances had been collected for some ewes in the 1952 flock.

Records taken for all lambs born include their respective identities, pedigrees, dates of birth, sex, birthcoat type, birthweight, type of birth and type of rearing. Collection of lamb data soon after birth minimises possible errors in their records; lambs not recorded for birthcoat before they are 3 days old are discarded from the experimental data.

Table 15 Description of birthcoat types

Symbol	Body regions showing a reduction in halo-hair density
1	A very dense cover of halo-hairs over the whole body
1b	A slight reduction on the sides of the neck
2a	Reduction covering the fore-part of the body except the shoulders or sides. The area on the heart, girth and behind the elbow shows a noticeable reduction
2	Neck, chest and shoulders practically free while sides show varying amounts of halo-hair densities
2c	Only the posterior quarter, lumbar and ventral regions show halo-hairs while the rest of the body is virtually free
3	The whole body practically free from halo-hairs. These can be found on the legs, belly and tail

Source: Adaptation from Purser and Karam, 1967

The initial birthcoat type assessment is done at the farm by recording the degree of halo-hair density over all body regions. A score from 2 to 7 is in use at Rhydyglafes to denote increasing halo-hair densities. These scores are written on a body profile of the lamb thus indicating the appropriate densities in different body regions. Each of these individual diagramatic records is later classified into one of the six classes mentioned in Table 15.

In order to perform statistical operations birthcoat grades must have certain values assigned to them and the problem of choice of scale for this trait was studied by Purser (unpublished). He suggested

Liveweights of lambs, hoggets and ewes are measured at different ages, all three groups being weighed at shearing and at weaning time while the last two groups have an additional weighing at tupping; a pre-tupping weight is recorded in October and a post-tupping weight in November.

In July, at the shearing gathering, fleece weights and fleece remarks are recorded and wool samples collected. Each fleece is judged for commercial quality by the British Wool Marketing Board.

2. Birthcoat type classification

Halo-hairs are the most conspicuous of birthcoat fibre types on account of their coarseness, wire-like straightness and relatively large size; these fibres project over the rest of the coat and when fairly dense they give a fluffy appearance to its outline. Coverage and density of halo-hairs show a definite pattern in their distribution over the body, and this characteristic has been used by several research workers to describe birthcoat type variability (White, 1925; Dry, 1934; Williams, 1948; Fraser and Short, 1960; Purser and Karam, 1967). It can be assumed that these patterns are related to body gradients reported for diverse characteristics of follicle and fibre population (Gaplin, 1935; Wildman, 1937; Young and Chapman, 1958).

Lambs at Rhydyglafes have been classified into one of six birthcoat types according to the spread of dense halo-hair over the body. A description of birthcoat types appears in Table 15 .

that the choice of values would be determined by the objectives pursued in the analysis and that the appropriate values for statistical analysis of data from a selection experiment would be those that maximised heritability estimates. Calculations indicated that a linear scale with values from 1 to 6 would satisfy this condition reasonably well. The proposed scale gave values 1 to Type 3 birthcoat and 6 to Type 1 birthcoat. For the sake of clarity the birthcoat types will be referred to subsequently on this scale of 1 to 6, Type 1 being the finest birthcoat type, Type 6 being the coarsest birthcoat type.

Birthcoat types were recorded in this flock for lambs born previous to the initiation of the selection experiment based on this trait. This information refers to lambs born in 1951 and 1952 and they provide an estimate of the initial frequency distribution for birthcoat type in this flock. Figures for these two lamb crops appear in Table 16.

Table 16 Distribution of birthcoat types before selection

Year of birth	Birthcoat types					
	1	2	3	4	5	6
Born 1951	-	2	10	14	31	90
Born 1952	-	1	4	5	18	107
Pooled data	-	3	14	19	49	197
Percentage	-	1.1	5.0	6.7	17.4	69.9

The figures given above indicate a clear predominance of dense, coarse and hairy birthcoats which appear in approximately 70% of the cases while the remaining 30% is formed by intermediate birthcoat types; no lambs were recorded in the extremely fine category in any of these years. The pooled data for 1951 and 1952 gave an average value of 5.5 for birthcoat type value in this flock.

3. Matings

Rhydyglafes ewes were grouped by age during Autumn 1952 and randomly assorted within age into two lines which became known as the High and the Low Line. These two lines have remained closed since the 1952 tupping; the only exception to this occurred in the 1959 tupping when all High line ewes which did not have Type 1 birthcoats were transferred to the Low line. This change of line involved 12 ewes and the total number of ewes in the Low line matings for 1959 was about 200.

Mass selection has been practised in this flock throughout the experiment. Extreme birthcoat types have been selected for in each line: coarse and hairy (Type 6) birthcoats in the High Line and conversely, fine and wodly (Type 1) birthcoats in the Low Line.

To insure against possible losses a first selection of 20 to 25 ram lambs has been practised in each line at two to three weeks of age; of these, 8 normally sired the next lamb crop. A further selection requisite has been to choose one ram from each sire progeny group of the previous year; this procedure of selecting within sire-groups helps to avoid inbreeding effects but reduces the response to selection. During the opening years mostly yearling rams were used but as ram lambs of approximately 7 months of age proved suitable as tups only ram lambs have been used since 1955.

Females have been culled mainly on management criteria, chiefly based on size and conformation, but some attention on birthcoat has been paid when culling individuals at 6 months of age.

The number of mating pairs for each line, within years, appears below in Table 17. The age and birthcoat type of rams is also presented.

Table 17 Description of sheep involved in each annual line mating

Year	Age of ram		Birthcoat value					No. of rams	No. of ewes
	Yearling	Lamb	1	2	3	4	6		
HIGH LINE									
1952	7	-				1	6	7	193
1953	8	-					8	8	204
1954	4*	4					8	8	190
1955	-	8					8	8	189
1956	-	8					8	8	228
1957	-	9					9	9	214
1958	-	8					8	8	193
1959	-	8					8	8	173
1960	-	9					9	9	191
1961	-	9					9	9	222
1962	-	9					9	9	192
1963	-	8					8	8	199
1964	-	9					9	9	192
1965	-	8					8	8	208
1966	-	8					8	8	198

Table 17 Continued

Year	Age of ram		Birthcoat value					No. of rams	No. of ewes
	Yearling	Lamb	1	2	3	4	6		
L O W L I N E									
1952	7	-	2	2	3			7	193
1953	8	-	1	3	4			8	197
1954	4	4	2	4	2			8	188
1955	-	8	1	3	4			8	197
1956	1	8	5	3	1			9	229
1957	-	8	5	3	-			8	217
1958	-	8	6	2	-			8	210
1959	-	8	8	-	-			8	202
1960	-	9	9	-	-			9	214
1961	-	8	7	1	-			8	177
1962	-	8	8	-	-			8	160
1963	-	9	9	-	-			9	178
1964	-	9	8	1	-			9	185
1965	-	8	8	-	-			8	194
1966	-	9	9	-	-			9	180

Note: *In 1954 one ram in the High Line was 2 years old

C. Results

Lamb data from this experiment shows a clear and consistent response to selection. Furthermore the rate of response has been in good agreement with the expected high heritability of birthcoat type.

1. Changes in mean birthcoat values

Frequency distributions for birthcoat types within selection lines show the effects of the present breeding method. Figures for both sexes are tabulated below for the first selected crop of lambs and for the eighth and fourteenth crop respectively.

Table 18 Birthcoat type frequency distributions

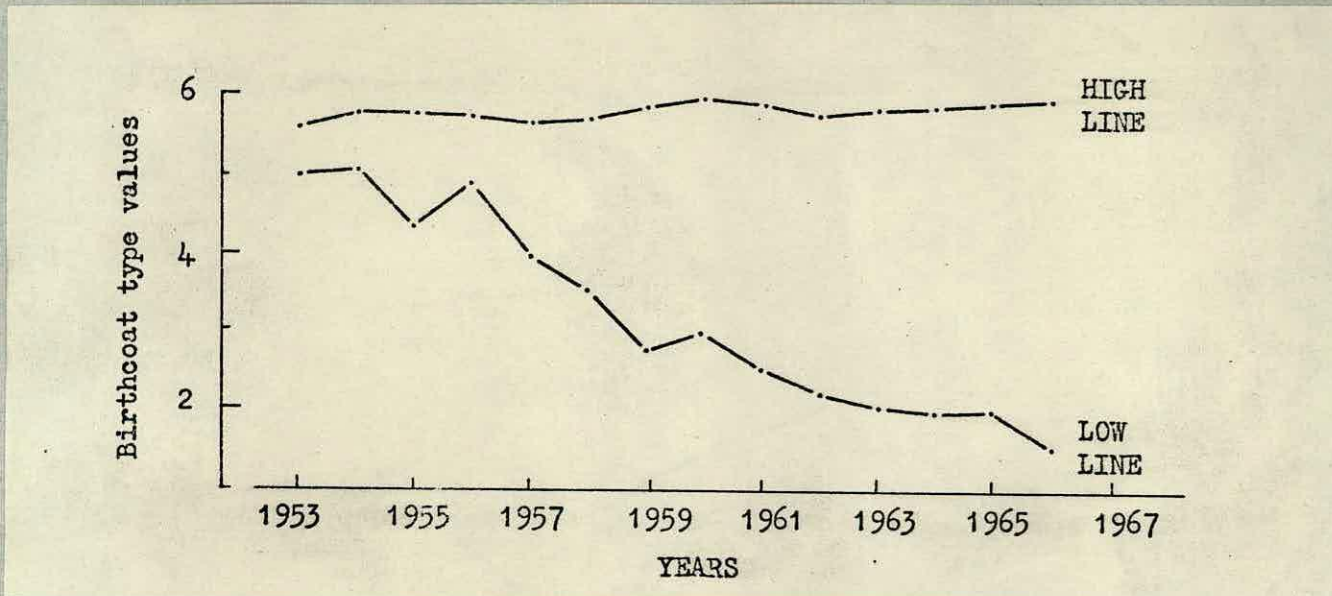
Year	Sex	High Line						Low Line					
		1	2	3	4	5	6	1	2	3	4	5	6
1953	♀	-	1	4	6	9	78	1	3	15	11	14	46
	♂	-	1	8	6	10	82	3	4	23	23	9	49
1960	♀	-	-	-	2	-	77	29	14	31	9	11	12
	♂	-	-	4	3	4	83	34	26	24	3	2	8
1966	♀	-	-	1	1	-	115	67	17	5	6	-	1
	♂	-	-	1	4	1	85	69	19	6	4	1	-

The figures presented above indicate a redistribution in birthcoat type frequency within selection lines, this being especially marked in the Low Line data.

The effects of selection can also be illustrated on the basis of birthcoat type averages for annual lamb crops within selection lines. These changes are shown in Figure 1.

FIGURE 1

Annual birthcoat average values of lambs

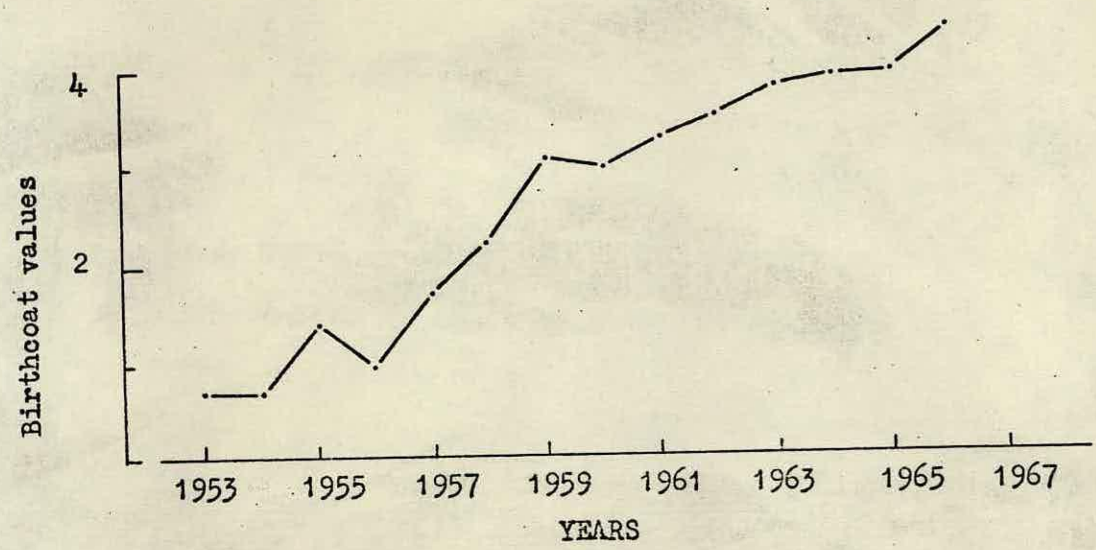


Progressive changes have occurred in both lines but a greater response has been shown by the Low line; an explanation for this difference lies in the lower selection ceiling possible in the High Line. The increasing line divergence with time suggests that selection for birthcoat has been effective. Line differences are highly significant for all years.

The absence of controls prevented the assessment of environmental effects on each selection line. Differences between lines can be regarded as an estimate of response with no environmental complications; the assumption here is that effects of environment are similar in both lines. Line differences plotted against years are shown on the next page in Figure 2.

FIGURE 2

Annual line differences in average birthcoat values of lambs



The above graph again shows the continuously increasing line difference as selection progresses.

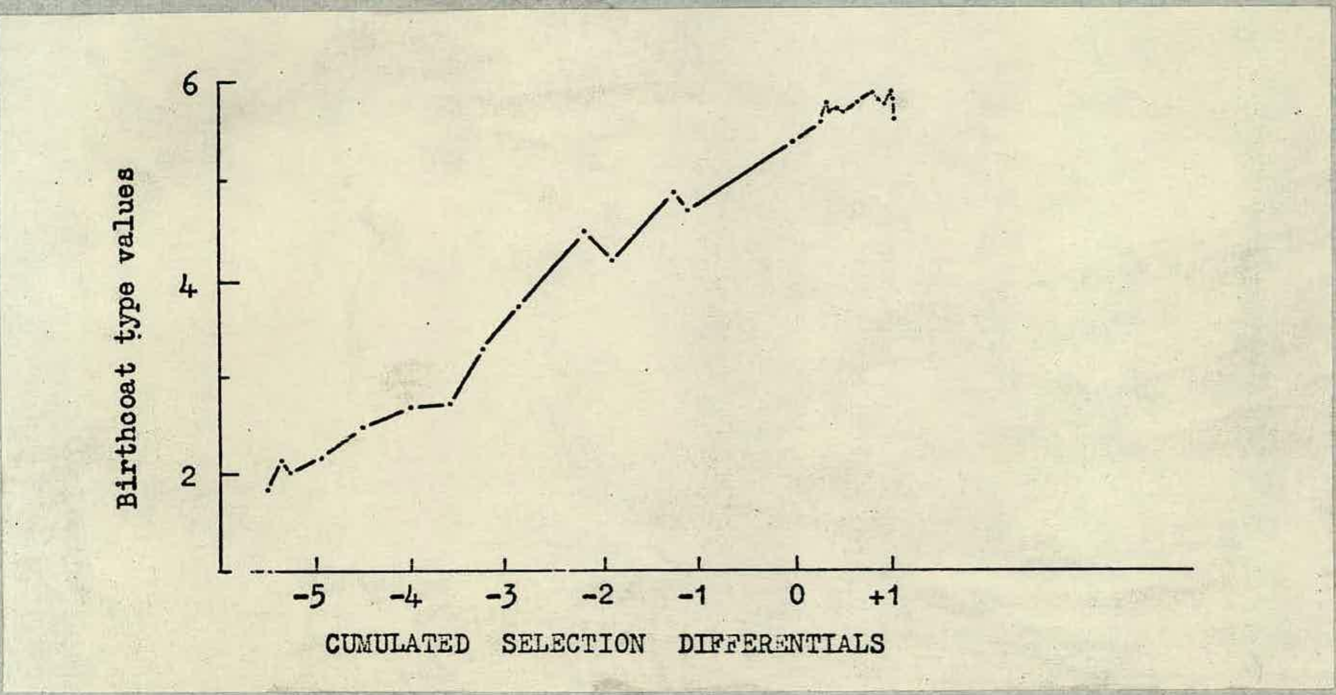
It also indicates differences in rates of response at different periods of the experiment, increments being small at the beginning and also slackening at the later stages while showing the bigger rates of change at the middle portion of the experimental period.

2. Heritability of birthcoat type

Purser (1967) has studied birthcoat type heritability using data from this experiment. Differences between annual line means for birthcoat type values were regressed on differences between annual line means for cumulated selection differentials; this led to estimates of realised heritability. Annual line differences for both these traits are graphically represented in Figure 3.

FIGURE 3

Regression of average line differences in birthcoat type on average line differences in cumulated selection differentials for lambs



The graph in Figure 3 shows the line differences in selection intensity; it also shows that the rate of response to selection tends to fall towards both extremes of the range while attaining a maximum at intermediate stages. The general slope for this curve is approximately 0.60 and it estimates the effective or realised heritability for birthcoat. The trend in response rates is similar to that of changes of mean values shown earlier in Figure 2 both indicating lower increments at the extreme points of the graph; this has been interpreted as suggesting that changes in additive genetic variance were closely connected to changes in mean values and thus related to gene frequency (Purser, 1967).

IV. MATERIALS AND METHODS

The basic information used in the present work was derived from two sources. The main experimental work was a detailed analysis of fleece samples from sheep belonging to the Rhydyglafes birthcoat selection experiment. This data was supplemented by information extracted from the routine records kept by the Animal Breeding Research Organisation, (A.B.R.O.).

A.- Materials.

1. Sheep Under Analysis

The fleece samples and the data to be analysed comes from 15 month old female sheep. Sheep up to this age are known, among other names, as hoggs or hoggets. Amongst these hoggets those born during the Spring of 1952, which became the 1953 hoggets, were unselected and they were later assigned at random to the High Line and the Low Line. Hoggets from 1954 to 1967 were all progenies from selected parents. A detailed description of the selection experiment and the farm conditions and the flock management was presented in the previous section.

2. Data Obtained Directly From A.B.R.O.'s Records

Routine records were available for all individual hoggets used in this study. These included pedigrees, birthcoat types, cumulated selection differentials, fleece weight and body weights for all hoggets and British Wool Marketing Board (B.W.M.B.) fleece grades for those born since 1957.

Birthcoat type classification included six grades and these were described in a previous section. Fleece weights represented 15 months of full wool growth and were weighed to the nearest tenth of a pound.

Commercial fleece grades were grouped according to the amount of kemp which is typical for each grade and with reference to prices.

Average prices for each fleece grade were calculated from official Price Schedules issued by the British Wool Marketing Board and on the basis of figures from 1962 to 1966. The following seven fleece grade groups are described in terms of the grades included in each group and their respective prices:

Group	Fleece grade	B.W.M.B. No.	Price: Pence/lb.
1:	Diamond Radnor	9653	69.5
	Deep half-bred hogg	9328	58.4
	Pick Radnor	9654	67.5
	Fine Radnor	9655	60.5
	Deep Radnor	9656	58.5
2:	Pick Welsh	9659	60.6
3:	Cast Radnor	9657	56.0
4:	Welsh grown scotch	9712-9715	55.1
	Kempy half-bred	9347	54.1
	Selected Welsh	9660	55.2
5:	Cast Welsh	9663	52.2
6:	Black Welsh	9690	46.6
	Red Kempy	9666	51.3
	Scotch grey	9792	48.3
7:	Light turbary	9665	41.0

3. Fleece Samples

Since 1953 all hoggets were fleece sampled and from 1958 inclusive these samples were taken from a measured area of 10 cm^2 on the mid-side and approximately at the last rib; the only exceptions in the later years of the experiment were 1961 and 1965 when plain samples from unknown areas of skin were collected. Fleece samples from the mid-side have been shown to be one of the most representative single regions for fleece sampling in Australian Merino sheep (Chapman and Young, 1957; Young and Chapman, 1958).

Amongst the available fleece samples those taken in 1953 and 1966 were chosen for a detailed fibre analysis. These two years were used as examples of two contrasting stages of the experiment, samples for 1953 representing the base population while those for 1966 were samples which showed the effects of approximately 6 1/2 generations of selection. In 1966 High and Low Lines showed an approximate divergence of 8.4 units in cumulated selection differential average values.

B. Methods used in the present study

This section will be sub-divided into a description of the methods used in the analysis of wool samples and those used in statistical computations.

1. Measurements

Direct measurements were performed at two levels: one which required wool samples to be handled as one whole piece, and which included dry wool weight per unit area of skin and staple length; and another in which a sub-sample of 100 to 120 fibres was taken from each wool sample, proceeding then to separate them into fibre types and finally recording fibre lengths, fibre diameters, fibre numbers and fibre weights. The former measurements

~~measurements~~ were essentially fleece characteristics and information was available for several years. The latter group of traits represented fibre characteristics and this analysis included only two years with a total number of 50 samples for 1953 and 142 for 1966.

(a) Dry wool weight per unit area

Wool samples were obtained from an area of 10 cm^2 of skin which was determined by using a standard caliper. These samples were oven dried for 6 hours at 100 to 105°C after placing them in open individual aluminium cannisters; once the drying period was completed the air tight screw top of each cannister was replaced and the samples were allowed to cool. Wool weight was determined by using an automatic balance and readings were recorded to the nearest milligram. This trait was on record for 7 years and it included 829 wool samples.

(b) Staple length

Wool samples were handled in such a way as to avoid any stretching and in order to obtain a guide to the depth of the fleece. Each individual sample was placed over a scale and readings were taken to the nearest half centimeter; the sample value was calculated as the average from three such determinations. The total number of wool samples measured for staple length from 1953 to 1967 was 1877.

(c) Fleece composition

Fibre types were classified into three categories: Kempy, Hairy and Woolly fibres. Kempy fibres show discontinuous growth which leads to shedding and all shed fibres present a constriction in their proximal end which terminates in a visible bulb-like structure; this morphological pecularity provides an easy and accurate method to differentiate kempy fibres from the other two types.

Hairy and woolly fibres show a continuous gradation in morphological characteristics so that the separation of these two types by naked eye inspection was based on certain arbitrary standards. Hairy fibres were usually very long with diameters above 40 µ, showing a very loose undulation with fairly large and deep curls along its length (loose crimp) and exhibiting medullation. When classifying by naked eye, fibre diameter and degree of medullation were assessed subjectively and this was done on the basis of the relative coarseness between fibres, by the presence of large and deep crimps and by a whitish opaque fibre colour. Woolly fibres showed finer diameters, under 40 µ, a very marked crimping with small sized but numerous curls along its length, and a translucid appearance.

A sub-sample containing some 100 to 120 fibres was carefully separated from each wool sample, following its longitudinal axis and ensuring that all fibres along the depth of the fleece were included. Each fibre was then allocated to its appropriate fibre type according to the description presented above.

Total number of fibres per fibre type was recorded for each individual and the relative contribution of kempy, hairy and woolly fibres to the total number of fibres were calculated.

The total weight of fibres per fibre type was recorded for each individual hogget and percentages were calculated for the relative contribution of kempy, hairy and woolly fibres in each sub-sample. The weights of fibre types was recorded to the nearest tenth of a milligram but when dealing with single fibres too light to be weighed a nominal weight of 10 µg was arbitrarily assigned to it.

(d) Fibre length

Individual fibres within fibre types were stretched on a scale and a single measurement was taken to the nearest half centimeter. All fibres, up to a maximum of 25, were measured for each fibre type within sub-samples, and the appropriate average values for kempy, hairy and woolly fibres were taken as the values for these traits for each hogget.

(e) Fibre diameter

Fibre cross-sections were obtained for each fibre type with the help of a Hardy microtome; these sections were then mounted on a slide and magnified 500 times using a projection microscope and measuring individual fibres to the nearest micron. Values for external and internal diameters were recorded. All the fibres, up to a maximum of 25, from each fibre type were measured and the appropriate averages were taken as the values for diameters of kempy, hairy and woolly fibres for each hogget.

Internal diameter readings were recorded in order to obtain information on medullation characteristics. Kempy fibres presented no problem because all of them showed continuous medulla. Hairy and woolly fibres did present certain complications because not all fibres were medullated; the average internal diameter for these fibres was calculated by dividing the total recorded for all these diameter readings, zero values included, by the total number of fibres. The calculations for average internal diameters for hairy and woolly fibres would, in this way, measure the extent of medullation incidence.

(f) Medulla types

Medulla types were recorded for hairy and woolly fibres. Three classes were used for hairy fibre medulla types: unbroken medulla, broken medulla and non-medullated types. Wool fibres fell into one of two classes: broken medulla, and non-medullated types. All figures were expressed as percentages.

Some of the measurements described above were used to derive estimates for the following fibre traits: average cortex area, average cortex volume, average weight and number of fibres per unit area. These derived measurements are described below.

(g) Average fibre weight

Estimates for weights of single fibres: kempy, hairy and woolly, were calculated from the total numbers and total weights recorded for each fibre type. These estimates were expressed in units of μg.

(h) Number of fibres per unit area or relative densities

Density figures were calculated for each hogget by using the following traits: the proportionate fibre type weights obtained for each sub-sample, the total dry wool weight per unit area and the average fibre type weight for single fibres. The figures for proportionate fibre type weight were used to sub-divide total dry wool weight per unit area into corresponding total sample weights for kempy, hairy and woolly fibres. These results were then appropriately divided by the average single fibre weight to give an estimate of fibre numbers per unit area. Relative densities were expressed as number of fibres per square centimeter.

2. Statistical Methods

The analysis of fleece and fibre measurements was basically similar but the small number of observations in the latter traits imposed limitations on their study.

Annual means and variances were computed for each trait within selection line and figures were also worked out for the overall pooled data.

Heritabilities, genetic correlations and phenotypic correlations were calculated for fleece and fibre trait measurements and birthcoat type, using a half-sib analysis. These estimates when related to birthcoat type were expected to show certain biases on account of the intense selection practiced on rams. Heritability and genetic correlation estimates were therefore, also calculated by daughter-dam regression analysis; estimates calculated by this method were expected to be biassed to a much lesser degree due to a considerably lighter selection pressure on females. Standard error for heritability estimates were based on the variance of intra-class correlation coefficient in the case of half-sib analysis and on the residual mean square in the case of daughter-dam regression. From here on half-sib analysis estimates will be referred to as HS estimates while DD estimates will be the abbreviated form for estimates from daughter-dam regression.

The amount of data for fibre traits was very limited and in the best of cases half-sib analysis included 16 sire progeny groups with a total of 142 hoggets; heritability and genetic correlation estimates were thus of little use on account of the large standard errors but this analysis did however provide estimates for some phenotypic correlations. Estimates for heritabilities and genetic correlations could not be calculated by daughter-dam regression because there were no fibre analysis information for consecutive generations.

The hoggets analysed in this study had been subjected to some selection for birthcoat type at the lamb stage. Their average birthcoat values were thus partly a measure of the average mid-parent breeding values and partly a measure of the phenotypic selection in that generation. Cumulative selection differentials (CSD) were available for each individual, these being calculated by adding the current selection differential to the mid-parent average selection differential, this calculation being continued back through the pedigree until the unselected base population was reached. The CSD combines the current and the previous selection on an equal footing, and would be expected to give a better indication of genetic differences between individuals than would birthcoat values themselves. Thus differences in CSD when multiplied by the heritability of birthcoat were assumed to represent differences in breeding value.

To analyse response to selection the differences between High and Low selection lines were calculated in each year for each trait available as well as for CSD. From here on these annual differences between lines for each particular trait will be referred to simply as line differences. The year means were assumed to be of equal weight and the values for each trait were regressed on the corresponding values of CSD. The regression coefficient was used in turn to estimate an "observed" genetic correlation coefficient.

The expected divergence between selected lines in the values of the unselected traits, *viz*. the correlated response (CR_y) can be shown to be (Falconer, 1960).

$$CR_y = i_x \; h_x \; h_y \; r_{G_{xy}} \; \sigma_y$$

where i_x = standardised selection intensity

h_y = square root of the heritability of the correlated trait

h_x = square root of the heritability of birthcoat type

$r_{G_{xy}}$ = genetic correlation between these two traits: x and y

and σ_y = phenotypic standard deviation in trait y

The CSD would have the value

$$CSD = i_x \; \sigma_x$$

and hence the regression of CR_y on CSD would be an estimate of:

$$b_{CR.CSD} = h_x \; h_y \; r_G \frac{\sigma_y}{\sigma_x}$$

By substituting values for the heritabilities and standard deviations an estimate of r_G is obtained.

In the case of fibre traits figures are only available for 1966 and the regression coefficient is merely the ratio of the average values in that year, assuming there were zero differences at the start of the experiment. Because no reliable estimates of heritability were available for these traits in this data values have had to be assumed and these have been generally taken to be 0.40 as most estimates in the literature are in the range 0.3 - 0.60.

Regression on CSD for the fleece traits were estimated in the usual way but dry wool weight presented a special problem since it was only recorded in the last few years. It seemed more appropriate to assume as with the fibre traits that there were no differences between the selection lines at the start of the experiment and thus assume the regression went through the origin. The same assumptions seemed reasonable for the other fleece traits and so for uniformity regressions through the origin are given for these also.

V. RESULTS

Fleece and fibre traits results will be reported separately because fleece trait measurements came from several years of the Rhydyglafes experiment while fibre traits represented only two: 1953 which was the starting point and 1966 which showed the effects of selection at an advanced stage.

A. Fleece Traits

1. Average values and variances

Means and variances were calculated for fleece weight, staple length and dry wool weight per unit area of skin; this was done within years and within lines. Similar computations were performed for birthcoat type values.

In order to give an idea of the level of performance of each trait, annual average values of High and Low Line were pooled and they appear in Table 19.

Table 19 Means and standard deviations for birthcoat and fleece traits

Year	No. obs.	Birthcoat type values	Fleece weight (lb.)	Staple length (cm.)	Dry wool weight (g/cm^2)
1953	88	5.66	2.81	9.42	-
1954	68	4.81	2.78	9.92	-
1955	152	5.28	3.01	9.67	-
1956	132	4.96	3.08	10.36	-
1957	116	5.32	3.41	10.12	-
1958	136	4.68	3.09	9.16	-
1959	135	4.49	3.06	9.54	0.288*
1960	135	4.01	2.70	9.64	0.252
1961	127	4.15	2.63	9.20	-
1962	131	3.98	2.96	9.77	0.231
1963	125	3.98	2.70	10.10	0.226
1964	128	4.09	3.17	9.94	0.246
1965	134	3.87	2.99	9.70	-
1966	142	3.68	2.85	10.04	0.249
1967	128	3.72	2.85	9.87	0.249
Pooled Values					
All years	1877	4.45	2.95	9.76	0.249
Standard deviations (within years)		1.09	0.59	1.70	0.045

Note: *1 Dry wool weight average for 1959 was based on 26 samples.

Fleece traits did not show much change from year to year but birthcoat type values indicate a steady decrease. Overall mean value for fleece weight was somewhat lower than average values reported by Dalton (1962) and Williams (1965) for first fleece weights in Welsh Mountain sheep. Rhydyglafes hoggets however showed longer staples than 20 month old Welsh ewes analysed in a study by Dalton (1962).

2. Genetic and Phenotypic Parameters

Heritabilities, genetic correlations and phenotypic correlations were calculated for fleece traits and birthcoat type by means of a half-sib analysis. Fleece weight, staple length and birthcoat type estimates were based on 193 sire progeny groups, which included a total of 1694 hoggets; dry wool weight estimates were based on 95 sire groups and 801 hoggets. Table 20 summarises these results.

Table 20 Half-sib estimates for fleece traits and birthcoat type

Traits	Birthcoat type	Fleece weight	Staple length	Dry wool weight
Birthcoat type	0.23 ± 0.08	-0.18	-0.19	-0.04
Fleece weight	0.02	0.56 ± 0.11	0.56	0.91
Staple length	0.04	0.43	0.55 ± 0.10	0.42
Dry wool weight	0.03	0.62	0.49	0.45 ± 0.13

Note: Values tabulated in the diagonal, from upper left to lower-right are the heritability estimates; those above are estimates of genetic correlations while those below it are phenotypic correlations.

Half-sib heritability estimates for fleece traits were high and some compared fairly well with previously reported figures (Dalton, 1962; Doney, 1958) for this breed. The birthcoat type estimate however was only about a third of the realised estimate worked out from lamb data belonging to the Rhydyglafes flock (Purser, 1967). This low estimate was thought to be caused by the reduction of variance amongst progeny groups on account of selection on rams.

Correlation values from the half-sib analysis showed negative genetic associations between birthcoat and fleece traits, most values being low. Phenotypic correlations however, were all positive and of negligible magnitude. Genetic and phenotypic correlations amongst fleece traits were all positive and most of them being of medium magnitudes.

Heritabilities and genetic correlations for fleece traits and birthcoat type were also calculated by daughter-dam regression. This set of estimates was based on 1363 pair of observations for birthcoat type, fleece weight and staple length, but only on 418 pairs for dry wool weight. Table 21 shows these estimates.

Table 21 Daughter-dam regression estimates for birthcoat and fleece traits

Traits	Birthcoat type	Fleece weight	Staple length	Dry wool weight
Birthcoat type	0.43 ± 0.02	0.17	0.04	0.16
Fleece weight		0.53 ± 0.02	0.53	0.96
Staple length			0.67 ± 0.02	0.53
Dry wool weight				0.44 ± 0.05

Note: The figures with standard errors are the heritability estimates; the others are genetic correlation estimates.

Estimates presented in Table 21 indicate substantial changes in values related to birthcoat type as compared to half-sib estimates but all other figures are remarkably similar. Heritability of birthcoat type is about twice the value obtained from half-sib analysis and all genetic correlations with fleece traits are positive.

3. Response to selection

Annual line differences for average values in each fleece trait illustrate the changes occurring between lines selected for the two extreme birthcoat types. These line differences are shown below in Table 22, together with corresponding values for birthcoat type and cumulated selection differential (CSD).

Table 22 Annual line differences

Year	Birthcoat type	Cumulated selection differential	Fleece weight (lb.)	Staple length (cm.)	Dry wool weight (g/cm^2)
1953	-0.04	0.00	0.06	-0.12	-
1954	0.88	1.42	0.06	0.07	-
1955	0.86	1.26	0.08	-0.02	-
1956	1.48	2.45	-0.10	0.54	-
1957	0.88	2.56	0.05	-0.24	-
1958	1.95	3.80	0.01	0.31	-
1959	3.05	4.26	0.04	0.66*	0.018
1960	3.83	5.10	-0.05	-0.34	0.008
1961	3.48	5.64	-0.06	0.97**	-
1962	3.91	6.41	0.03	0.63**	0.013
1963	3.52	7.03	-0.08	0.33	0.003
1964	3.95	7.70	0.44***	1.29***	0.029***
1965	4.05	8.09	0.37***	1.11***	-
1966	4.15	8.40	0.21	0.89***	0.028**
1967	4.57	8.79	0.07	0.76*	0.020*

Note: Throughout these results the statistical significance of estimates is indicated as follows:

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

Annual line differences in cumulated selection differentials for these hoggets show that selection pressure for birthcoat type has been persistent and that its cumulated values had increased quite consistently from year to year; similarly differences in birthcoat type values showed progressive increases in consecutive years. Results for cumulated selection differentials and birthcoat type from lamb data reported by Purser (1967) showed similar trends in average line values and this suggests that from birth to 15 months of age little changes occur in the selection effects.

Figures given in Table 22 show that all fleece traits indicate some significant line differences from 1964 onwards but from the available data only staple length seems to indicate a consistent trend in differences between average values for High and Low lines.

Correlated responses in fleece traits were tested by the regression of annual line differences, which appear in Table 22, on the corresponding differences in cumulated selection differentials. Table 23 show the results for the regression analyses for each fleece trait. Two regression coefficient estimates are presented: the ordinary coefficient b_{mean}, and another which assumes no High - Low differences in fleece traits at the beginning of the experiment, b_{origin}.

Table 23 Estimates of regression coefficients between birthcoat type and fleece traits

Regression coefficients	Fleece weight	Staple length	Dry wool weight
b_{mean}	0.029 ± 0.013	0.127 ± 0.003	0.0013 ± 0.0024
b_{origin}	0.017 ± 0.007	0.104 ± 0.020	0.0024 ± 0.0005

Both sets of regression estimates presented in Table 23 provide similar results and all b_{origin} estimates are statistically significant. These results suggest that changes for all fleece traits are significantly related to selection pressure for birthcoat type.

4. Observed and Expected Responses to Selection

Estimates for genetic correlations were used to compare observed and expected correlated responses. Observed genetic correlations were provided by the actual changes in line average values, the heritability estimates for the traits under study and the standard deviations of these traits. Values for expected genetic correlations came from HS and DD estimates. Table 24 gives the values for each of these three sources of estimation.

Table 24 Estimates of genetic correlations between birthcoat type and fleece traits

Source of estimation	Fleece weight	Staple length	Dry wool weight
HS estimates	-0.18	-0.19	-0.04
DD estimates	0.17	0.04	0.16
Observed: b_{origin}	0.06	0.12	0.12

The sets of estimates provided by the half-sib analysis contrast markedly with those provided by daughter-dam, and observed genetic correlation, while the latter show certain degree of agreement. There were no strong associations in any of the three sets of estimates.

B. Fibre traits

1. Phenotypic association with birthcoat type

Mean values within birthcoat type were calculated for all fibre traits measured from wool samples collected in 1966. In this set of samples extremely hairy birthcoats with value 6 were only found in the High Line, and all individuals sampled in this line had birthcoat type 6.

Mean values for fleece composition were based on relative numbers of kempy, hairy and woolly fibres, and also on relative fibre weight contributed by each of these fibre types. In addition to this tabulation of mean values a phenotypic correlation estimate was computed, the results of these calculations being shown in Table 25.

Table 25 Phenotypic association between fibre composition and birthcoat type: wool samples for 1966

Items		Birthcoat types					
	r_p	1	2	3	4	5	6
No. of Hoggets:		29	31	13	3	-	66
Fleece comp:							
(a) By numbers							
Kempy, %	0.20	0.0	1.0	1.9	5.7	-	12.0
Hairy, %	0.39	0.0	0.0	0.0	1.5	-	2.2
Woolly, %	-0.17	100.0	99.0	98.1	92.8	-	85.8
(b) By weight							
Kempy, %	0.13	0.2	0.8	2.6	5.4	-	15.5
Hairy, %	0.18	0.1	0.9	0.0	2.0	-	4.4
Woolly, %	-0.11	99.7	98.3	97.4	92.6	-	80.4

Note: r_p stands for phenotypic correlation with birthcoat type

Average values within birthcoat type and phenotypic correlations in samples for 1966, indicate that fleece composition is associated with birthcoat type classification. Kempy and hairy fibres tend to increase in their relative contributions with coarser birthcoat types while woolly fibre show the opposite trend.

Mean values within birthcoat type were also computed for fibre length, external and internal fibre diameter, fibre weight and incidence of different medulla types. These are shown in Table 26 along with estimates of phenotypic correlation with birthcoat score.

The number of hoggets within birthcoat type groups was generally on a limited scale with the sole exception of birthcoat type 6 which showed reasonable number of hoggets carrying kempy, hairy and woolly fibres. This limitation was most prominent within hairy fibres where only one hogget provided information for birthcoat types 1, 2 and 4; because of this restriction no reliable information could be found for trends in average values of this fibre type with birthcoat type classification.

Kempy fibres were the only fibre types which appeared to show some association with birthcoat type. Definite trends in average values for different birthcoat types were found in length, external and internal diameters, all of them increasing with coarser birthcoat types. Weight of kempy fibres indicated that, in general, a similar but less consistent trend was also present in this trait. Phenotypic correlations with birthcoat type appeared

Table 26 Phenotypic association between birthcoat type and fibre traits: wool samples for 1966

Item	r_p	1	2	3	4	5	6
No. Hoggets:							
Kempy		8	19	10	2	-	66
Hairy		1	1	-	1	-	39
Woolly		29	31	13	3	-	66
Length, cm.:							
Kempy	0.1	1.5	1.6	1.8	2.2	-	3.7
Hairy	-0.0	18.0	20.0	-	14.0	-	8.4
Woolly	0.0	12.4	13.2	11.9	14.0	-	10.1
Ext. diameter, µ:							
Kempy	0.5	73.8	77.3	91.0	94.5	-	104.0
Hairy	0.1	28.0	42.0	-	40.0	-	57.6
Woolly	0.1	23.3	24.1	22.2	23.5	-	23.6
Int. diameter, µ:							
Kempy	0.6	53.6	59.9	74.5	82.5	-	91.0
Hairy	0.0	0.0	12.0	-	4.0	-	33.2
Woolly	-0.0	0.2	0.6	0.3	0.0	-	0.8
Fibre weight, µg:							
Kempy	0.2	39.6	61.4	96.7	83.3	-	94.3
Hairy	0.3	300.0	331.3	-	100.0	-	140.5
Woolly	0.1	82.4	98.4	87.7	96.2	-	74.0
Medullated hairs:							
% Unbroken	0.0	0.0	56.3	-	14.3	-	98.4
% Broken	1.0	0.0	18.7	-	57.1	-	0.0
% Non-medullated	0.7	100.0	25.0	-	28.6	-	1.6
Medullated wool:							
% Broken	-0.0	0.9	1.6	1.1	0.0	-	1.5
% Non-medullated	0.0	99.1	98.4	98.9	100.0	-	98.5

to be of some importance for both fibre diameters but length and fibre weight indicated low values for this parameter.

Woolly fibres showed no consistent trends in their average values for different birthcoat types and the only correlation values found were for external diameter: 0.1, cortex area: -0.1 and fibre weight: 0.1, all of them of negligible magnitudes.

2. Response to Selection in Fibre Traits

Differences in average values for fibre traits between High and Low selection lines were studied in two years: 1953 and 1966.

Fleece composition was described in terms of relative numbers of kempy, hairy and woolly fibres and also in terms of the relative total fibre weight contributed by each of these fibre types. Wool samples for 1953 came from 25 hoggets in each selection line while those for 1966 came from 66 High Line hoggets and 76 Low Line hoggets. Mean values for each line in both years, and differences between High and Low lines are tabulated in Table 27.

Fleece composition results for 1966 showed highly significant differences between High and Low lines in the number and the weight of fibres contributed by kempy, hairy and woolly fibre types. Kempy and hairy fibres had higher average values in the High Line but woolly fibres gave higher average values in the Low Line.

Table 27 Fleece composition: 1953 and 1966

Year	Line	Line mean values			Items	Line differences		
		Kempy	Hairy	Woolly		Kempy	Hairy	Woolly
				Total number of fibres per fibre type, %				
1953	High	10.9	5.8	83.3	Diff.	0.8	0.0	0.8
	Low	10.1	5.8	84.3	S.E.	1.9	1.2	2.3
1966	High	12.0	2.2	85.8	Diff.	10.9**	2.0**	-13.0**
	Low	1.1	0.2	98.8	S.E.	0.6	0.3	2.4
				Total fibre weight per fibre type, %				
1953	High	12.0	15.4	72.6	Diff.	3.2	0.5	-3.7
	Low	8.8	14.9	76.3	S.E.	2.2	3.4	4.1
1966	High	15.5	4.4	80.1	Diff.	14.5**	3.9	-18.4**
	Low	1.0	0.5	98.5	S.E.	1.2	2.9	1.5

Line differences in fleece composition indicate that High and Low Line groups were very similar in 1953 but that significant line differences were present in wool samples for 1966.

Mean values for fibre traits were calculated from observations on samples collected in 1953 and 1966. The following traits were included: fibre length, internal and external fibre diameter, fibre weight and incidence of different medulla types. Mean values for each fibre type are presented in Table 28.

Table 28 Line mean values for fibre traits in 1953 and 1966

Items	Kempy		Hairy		Woolly	
	1953	1966	1953	1966	1953	1966
No. of Hoggets:						
HIGH	24	66	21	39	25	66
LOW	25	39	21	3	25	76
Fibre length, cm.						
HIGH	3.6	3.7	14.0	8.4	10.8	10.1
LOW	3.4	1.6	14.6	17.3	10.8	12.7
Ext. fibre diam., µ						
HIGH	87.4	104.0	42.8	57.6	24.0	23.6
LOW	86.0	81.0	40.9	36.7	23.0	23.5
Int. fibre diam., µ						
HIGH	72.9	91.0	11.8	33.2	0.4	0.8
LOW	72.5	63.5	10.2	5.3	0.3	0.4
Medulla types:						
Unbroken %						
HIGH	-	-	59.0	98.5	-	-
LOW	-	-	57.1	23.5	-	-
Broken, %						
HIGH	-	-	16.3	0.0	1.2	1.5
LOW	-	-	16.9	25.3	0.7	1.2
Non-med., %						
HIGH	-	-	24.7	1.5	98.8	98.5
LOW	-	-	26.0	51.2	99.3	98.8
Fibre weight, µg						
HIGH	99.3	94.3	253.0	140.5	77.7	74.0
LOW	69.1	67.1	221.6	243.8	74.9	90.3
Fibre density No./cm^2						
HIGH	-	419.0	-	77.0	-	3066.0
LOW	-	26.0	-	5.0	-	2696.0

Table 29 Line differences for fibre traits in 1953 and 1966

Items	Kempy		Hairy		Woolly	
	1953	1966	1953	1966	1953	1966
No. of Hoggets:						
HIGH	24	66	21	39	25	66
LOW	25	39	21	3	25	76
Fibre length, cm.						
Diff.	-0.2	2.1***	- 0.6	- 8.9**	0.0	- 2.6***
S.E.	0.3	0.2	1.6	3.5	0.9	0.6
Ext. fibre diam. µ						
Diff.	1.4	23.0***	1.9	20.9*	1.0	0.1
S.E.	6.9	5.4	1.8	10.3	0.7	0.4
Int. fibre diam. µ						
Diff.	0.4	27.5***	1.6	27.9**	0.1	0.4**
S.E.	7.1	5.4	1.8	12.7	0.2	0.15
Medulla types:						
Unbroken, %						
Diff.	-	-	1.9	74.9***	-	-
S.E.	-	-	8.1	5.4	-	-
Broken, %						
Diff.	-	-	- 0.6	- 25.3***	0.5	0.3
S.E.	-	-	4.8	3.3	0.4	0.4
Non-med., %						
Diff.	-	-	- 1.3	- 49.6***	-0.5	- 0.3
S.E.	-	-	7.4	7.4	0.4	0.4
Fibre weight, µg						
Diff.	30.1**	27.2**	31.4	-103.3	2.8	-16.3
S.E.	12.4	12.4	69.9	69.9	5.8	14.0
Fibre density, No./cm^2						
Diff.	-	393.0**	-	72.0**	-	370.0**
S.E.	-	23.0	-	12.0	-	135.0

Mean values for fibre traits shown in Table 28 indicate clearly that High and Low Line values in 1953 are very similar but comparisons for 1966 data provide widespread line differences. Table 29 gives line differences for all fibre traits and shows if they are statistically significant.

Figures for line differences in 1953 indicate that only kempy fibre weight was significantly different between High and Low Lines. Data for 1966 however, showed highly significant line differences in all kempy fibre traits, almost all hairy fibre traits and in length and internal fibre diameter of woolly fibres.

Line differences in fibre traits (CR_y) were related to High-Low differences in cumulated selection differentials (CSD). The ratio between these two differences was assumed to estimate the regression coefficient relating changes in fibre traits with selection pressure. The values for these ratios appear in Table 30; the approximate value of differences in CSD for 1966 data was 8.4.

Table 30 Regression coefficient estimates of fibre trait line differences on similar differences in cumulated selection differentials

Traits	Line Differences			Regression Coefficient		
	Kempy	Hairy	Woolly	Kempy	Hairy	Woolly
Fleece composition:						
(a) Number of fibres	10.9**	2.0**	-13.0**	1.30	0.24	-1.54
(b) Weight of fibres	14.5**	3.9**	-18.4**	1.72	0.46	-2.19
Fibre length	2.1**	- 8.9**	- 2.6**	0.25	- 1.06	-0.31
Ext. fibre diameter	23.0**	20.9**	0.1	2.74	2.49	0.01
Int. fibre diameter	27.5**	27.9**	0.4**	3.27	3.32	0.05
Fibre weight	27.2**	-103.3	16.3	3.24	-12.29	1.94
Medulla types:						
% Unbroken	-	74.9**	-	-	8.92	-
% Broken	-	- 25.3**	0.3	-	- 3.01	0.04
% Non-med.	-	- 49.6**	- 0.3	-	- 5.90	-0.04

3. Observed genetic correlations of fibre traits with birthcoat type

Estimates for observed genetic correlations were calculated using the following factors: (a) the regression coefficient of line difference (CR_y) on differences for CSD, (b) heritability estimates of 0.60 for birthcoat type and an assumed value of 0.4 for heritability of fibre traits and (c) phenotypic standard deviation estimates for birthcoat type (Low Line value) and fleece traits. Results appear in Table 31.

Table 31 Estimates for observed genetic correlations of fibre traits with birthcoat type

Traits	Genetic correlation coefficient		
	Kempy	Hairy	Woolly
Fleece composition			
(a) Number of fibres	0.87	0.28	-0.82
(b) Weight of fibres	0.59	0.19	-0.56
Fibre length	0.68	-0.52	-0.21
Ext. fibre diameter	0.23	0.40	0.00
Int. fibre diameter	0.28	0.45	0.01
Fibre weight	0.16	-0.30	0.16
Medulla types			
% Unbroken	-	2.80	-
% Broken	-	-1.55	0.05
% Non-medullated	-	-1.36	-0.05

Results reported in Table 31 indicate that birthcoat type is positively correlated with all kempy fibre traits and several hairy fibre traits; however, negative correlation coefficients were found for birthcoat type with the following hairy fibre traits: fibre length, fibre weight and for both incidence of broken medulla and non-medullated hairy fibres. Estimates for the last two traits just mentioned gave values outside the normal range for correlation coefficients. Birthcoat type showed negative correlation coefficients with woolly fibre contributions to fleece composition and woolly fibre length.

C. Commercial fleece grades

1. Phenotypic description of fleece grades

Fibre characteristics and other materials included in fleeces determine their commercial value. On the farm the commercial quality and value of the fleece is visually assessed by tradesmen and assigned to one of a limited number of grades. These grades in turn determine the price paid to the farmer.

The hogget fleeces had been graded by the British Wool Marketing Board since 1958 but in 1966 in particular it was possible to compare these grades with the fleece and fibre traits in the samples. Fleece grades for this year appeared in groups 1, 4, 5, and 6 of the 7 quality groups. Group 1, the best quality group, was made up of Radnor type fleeces; group 4 was represented virtually by Selected Welsh fleeces; Group 5 was represented only by cast Welsh fleeces and Group 6 was formed by coloured fleeces. Mean values for fleece and fibre composition for each B.W.M.B. commercial grade are given in Tables 32 and 33.

Mean values tabulated in Table 32 suggest that comparatively shorter staple lengths and lower incidence of kempy and hairy fibres seem to be the most noticeable features in visual assessment of fleece quality.

Table 32 Phenotypic associations between fleece quality groups and fleece traits: wool samples for 1966

Items	Fleece		Quality		Group	
	1	2 & 3	4	5	6	7
No. of Hoggets:	70	-	47	11	14	-
Fleece wt.: lb.	2.7	-	3.1	2.9	2.8	-
Staple length: cm.	9.5	-	10.5	10.1	10.7	-
Dry wool wt.: g/cm^2	0.233	-	0.267	0.272	0.254	-
Fleece comp.:						
(a) By numbers:						
Kempy	1.4	-	10.8	6.3	13.7	-
Hairy	0.2	-	2.2	0.5	3.1	-
Woolly	98.4	-	87.0	93.1	83.2	-
(b) By weight:						
Kempy	1.3	-	13.7	9.0	19.0	-
Hairy	0.4	-	4.0	1.2	7.3	-
Woolly	98.3	-	82.3	89.8	73.7	-

Radnor type fleeces, compared with the other three quality groups, showed substantially shorter staples and virtual absence of kempy and hairy fibres. The same two traits differed amongst the other three groups but to a much lesser degree as compared to differences reported above for group 1. Staple length and incidence of kempy and hairy fibres increased among other groups in the following order:

from cast Welsh (Group 5) through Selected Welsh (Group 4) to coloured fleeces (Group 6.)

Average values for fibre traits within fleece quality groups were also derived from data for 1966. These mean values appear in Table 33.

Table 33 Phenotypic associations between fleece quality groups and fibre traits: wool samples for 1966

Items	Fleece quality groups					
	1	2 & 3	4	5	6	7
No. of Hoggets:	70	-	47	11	14	-
Kempy	38	-	44	9	14	-
Hairy	5	-	24	3	10	-
Woolly	70	-	47	11	14	-
Length, cm.:						
Kempy	1.8	-	3.6	2.5	4.2	-
Hairy	13.2	-	8.9	9.7	7.2	-
Woolly	12.3	-	11.4	9.7	9.0	-
Ext. diam.: u						
Kempy	79.3	-	100.8	105.4	115.8	-
Hairy	42.4	-	58.4	56.3	57.5	-
Woolly	23.5	-	23.5	23.4	23.3	-
Int. diam., u:						
Kempy	62.3	-	87.8	90.9	102.1	-
Hairy	15.2	-	34.4	27.7	32.4	-
Woolly	0.4	-	0.9	0.4	0.6	-
Fibre wt., ug:						
Kempy	63.7	-	91.1	103.7	105.9	-
Hairy	188.0	-	131.4	169.4	160.8	-
Woolly	87.7	-	79.2	80.5	71.5	-
Medullated hairs:						
% Unbroken	62.9	-	96.8	100.0	97.3	-
% Broken	11.4	-	0.8	0.0	0.0	-
% Non-medullated	25.7	-	2.4	0.0	2.7	-
Medullated wool:						
% Broken	1.2	-	1.6	1.1	1.1	-
% Non-medullated	98.8	-	98.4	98.9	98.9	-

The comparison of readily noticeable fibre traits among the different fleece quality groups show that Radnor type fleeces (Group 1) are associated with much shorter and thinner kempy fibres, longer but thinner hairy fibres and longer woolly fibres. The differences for these fibre traits among the three remaining groups indicate that hairy fibres are longest in Cast Welsh fleeces (Group 5) and shortest in Coloured fleeces (Group 6) while woolly fibres decrease in length from Selected Welsh (Group 4) through Cast Welsh to Coloured fleeces.

2. Phenotypic association of fleece grades with birthcoat type

Figures for the distribution of birthcoat type within fleece quality groups were tabulated to illustrate the type of relationship between both traits. This tabulation appears below and comes from data of 1966.

Table 34. Association of commercial fleece quality groups with birthcoat type

Birthcoat type	1	2 & 3	4	5	6	7
1	26	-	2	1	-	-
2	28	-	3	-	-	-
3	8	-	1	4	-	-
4	2	-	1	-	-	-
5	-	-	-	-	-	-
6	6	-	40	6	14	-

The distribution of the above figures points out the fact that higher commercial fleece quality seems to be associated with fine birthcoat type (Type 1). Radnor type fleece group was the only group where fine birthcoat type predominated while in the other three fleece groups hairy birthcoat type (Type 6) prevailed. Differences in birthcoat type composition amongst Selected Welsh, Cast Welsh and Coloured fleeces were contributed by minor differences in relative numbers of intermediate and fine birthcoat types.

3. Response to Selection

Differences between High and Low Lines in commercial fleece grades were described by means of annual frequency distribution for this trait in each line. Table 35 gives the frequency distribution of fleece quality groups by selection line for each year since 1958.

The results shown in Table 35 indicate that after 5 years of selection (2 generations), in 1958, High and Low Line distributions were already different; the Low Line, in contrast to the High Line, included a considerable number of good fleeces, Group 2. These differences between lines are progressively enhanced in successive years so that results for 1967 show almost no overlap in the distribution of fleece quality groups.

Table 35. Line frequency distributions for fleece quality groups: 1958-67

Line	Year	B.W.M.B. fleece grade groups: %						
		7	6	5	4	3	2	1
High	1958	2.9	4.4	2.9	82.9	-	7.4	-
	1959	32.8	11.5	14.8	39.3	-	-	1.6
	1960	-	2.9	2.9	84.1	-	10.1	-
	1961	-	14.5	16.1	69.4	-	-	-
	1962	-	4.5	9.0	74.6	-	1.5	10.4
	1963	-	14.0	10.0	70.0	-	-	6.0
	1964	-	5.7	12.9	71.4	1.4	-	8.6
	1965	-	17.2	34.5	32.8	10.3	-	5.2
	1966	-	21.2	9.1	60.1	-	-	9.1
	1967	-	44.8	11.9	37.3	4.5	-	1.5
Low	1958	3.0	3.0	1.5	45.5	-	42.4	4.6
	1959	23.0	1.6	11.5	23.0	-	16.4	24.6
	1960	-	-	-	27.3	-	50.1	16.7
	1961	-	1.6	-	46.9	-	20.3	31.2
	1962	-	-	-	12.5	-	31.3	56.2
	1963	-	1.6	4.8	19.0	17.5	1.6	55.5
	1964	-	-	3.5	15.5	3.4	8.6	69.0
	1965	-	-	3.1	1.5	20.0	-	75.4
	1966	-	-	6.6	9.2	-	-	84.2
	1967	-	-	-	-	32.8	-	67.2

As a more convenient means of analysing fleece quality it was decided to combine the fleece grade figures by assigning a scale value to each one. Prices per pound for individual fleece grades seemed the most appropriate values to use; a standard average price was used for all years involved in the analysis. Annual line differences in average price per pound of fleece were regressed on corresponding CSD differences; similarly annual line differences in average price for the total fleece per hogget, thus taking in consideration the differences in fleece weight/hogget as well, were also regressed on CSD differences. These two regression analyses attempted to relate changes in wool quality and total economic return per hogget, respectively, with the amount of selection practised on this flock. Results for these analyses are presented in Table 36.

Table 36. Regression of line differences for commercial fleece quality on CSD differences

	Average price/lb.	Average price for total fleece/hogget
$b_{mean} \pm$ S.E.	-0.621 ± 0.24	1.415 ± 1.78
$b_{origin} \pm$ S.E.	-0.685 ± 0.063	-1.029 ± 0.495

The b_{origin} regression coefficients indicate a significant negative correlation of birthcoat type with fleece quality as well as with total economic return per hogget.

VI. DISCUSSION

Data in the present study comes from hoggets in a flock under continued selection for extreme birthcoat types. Response to selection for this trait has been quite consistent and in good agreement with theoretical expectations (Purser, 1967). The present hoggets are female lamb survivors up to 15 months of age and they had a birthcoat type distribution that was very similar to that of lamb data. This suggested that selection effects would probably show little or no changes between the two life stages. The interpretation of correlated responses, on the other hand, is slightly more involved on account of the possible phenotypic correlations between birthcoat type and unselected traits, as well as for possible biases introduced in the calculation of genetic parameters.

The differences between High and Low lines in any one year with regard to any one trait, hereafter referred to as line differences, comprise ~~of~~ genetic differences as well as ~~of~~ differences arising between the groups on account of environmental correlations of the trait with the birthcoat type. Estimates for regression of annual line differences on corresponding differences between High and Low Lines in cumulated selection differentials of birthcoat type, hereafter referred to as CSD differences, provide a guide to genetic changes between selection groups.

Calculations for genetic parameters may be affected, among other things by the amount of selection practiced on any material; estimates calculated by paternal half-sib analysis (HS estimates) for the present hogget data, for example, give genetic parameters related to birthcoat type which seem to be seriously affected by selection practiced on parents. Heritability estimates for birthcoat type illustrate this point very clearly. Paternal HS estimates, as expected, provide the lowest heritability figure of 0.23, for it is in this type of analysis where reduction of birthcoat type variability between sire progeny is likely to be highest on account of the strong selection pressure practiced on rams. Estimates obtained by daughter-dam regression analysis (DD estimates), where selection pressure on breeding ewes is much lighter, gave a higher value of 0.43. Estimates of realised heritability derived from lamb data belonging to Rhydyglafes flock provides a figure of 0.60 (Purser, 1967); here the effects of selection on parents are accounted for and do not bias the estimate of heritability. This last estimate agrees well with other high heritability estimates reported by Rendel (1954), Morley (1955) and Schinckel (1955). The comparison of results derived by different methods indicates that genetic parameters from DD estimates should provide more reliable information than those from HS estimates; the former estimates would nevertheless still show limitations imposed by the selection practiced in the flock. The comparatively lower estimate of heritability obtained by DD regression is supported by the work of Brown and Turner (1968) on the effects of selection, for clean wool weight, in Australian Merino sheep; they concluded that after selection a reduction in additive genetic variance has occurred, though the changes could not be as yet tested for statistical significance. Maternal effects can also introduce biases in DD estimates but this seems unlikely in the case of birthcoat type.

A. Fleece traits

Line differences in fleece weight, staple length and dry wool weight per unit area of skin were significantly correlated to CSD differences. This indicates that selection for birthcoat type has caused correlated changes in fleece traits. The magnitude of these changes was nevertheless small and after seven generations of selection line differences for fleece weight, staple length and dry wool weight were expected to be 5% 9% and 8%, respectively, of the mean values for these traits pooled over all years.

Genetic correlation coefficients between birthcoat type and fleece traits were calculated. Observed and DD estimates gave positive values of negligible magnitude randing from 0.04 to 0.17 while HS estimates gave negative but also negligible values in the range of -0.04 to -0.19. The former estimates are in agreement with Morley (1955) who found a significant positive genetic correlation of birthcoat type with fleece weight and a positive but non-significant correlation with staple length. Results reported by Purser and Karam (1967) for adult ewes at Rhydyglafes are, on the other hand, in agreement with the HS estimates presented here; they reported values of -0.40 for HS estimates and -0.28 for DD estimates for the genetic correlation coefficient between birthcoat type and fleece weight.

Phenotypic correlations of birthcoat type with fleece weight, staple length and dry wool weight indicated virtual independence between these two traits; the correlation coefficients were calculated, by half-sib analysis within lines, from data pooled over all years. Purser and Karam

(1967) also reported a lack of correlation between birthcoat type and fleece weight in adult Welsh mountain ewes. The data of Schinckle (1958) on Australian Merino sheep and of Wilson et al. (1962) on Rambouillet, Targhee and Columbia sheep also indicated absence of any phenotypic correlations between birthcoat type and fleece weight or staple length. Morley (1955), working with Australian Merino sheep, reported a significant, though negligible correlation coefficient for birthcoat type with fleece weight but no correlation with staple length. All these results suggest that phenotypic correlations between birthcoat type and fleece traits are negligible and for all practical purposes, these traits could be considered as independent. This conclusion is in contrast with the presence of genetic correlations between these traits. The reason for this discrepancy is uncertain.

Genetic and phenotypic correlations were also calculated amongst fleece traits. Genetic correlations were calculated by HS as well as DD estimates, and both the estimates gave remarkably similar values of medium to high magnitudes. The phenotypic correlation coefficients were all of medium magnitude, from 0.4 to 0.6. The finding of positive correlations amongst various fleece traits considered here can therefore be of value in future sheep breeding programmes.

b. Fibre traits

Various traits concerning kempy, hairy and woolly fibre types were analysed in fleece samples from unselected hoggets, for 1953 as well as from hoggets after $6\frac{1}{2}$ generations of selection (8.4 units of CSD differences), for 1966.

In general results for 1953 indicated no line differences while most traits showed highly significant line differences for 1966 data, indicating that responses to selection were present in fibre traits. These correlated responses were of large magnitude and affected all traits in kempy and hairy fibres, with the exception of hairy fibre weight. Woolly fibres appeared less affected by selection pressure. These observations could be explained as follows. In Australian Merino sheep it has been suggested that the changes in birthcoat type were related to changes in the activity of primary follicles, but no significant effects could be seen on secondary follicles (Lockhart 1956, Schinckel, 1958). In the light of the above observations it is reasonable to assume that kempy and hairy fibres, because of their growth from primary follicles (Carter, 1955; Ryder, 1965), would be the ones most affected by selection for birthcoat type; while almost all the woolly fibres, because of their development from secondary follicles, would not be so affected. The work of Short (1951) on several Welsh Mountain sheep is also in agreement with the present findings; he found that in sheep types where most lambs have hairy and coarse birthcoat, the adult fleeces were heavily kemped.

The observed genetic correlation coefficients between birthcoat type, and various kempy and hairy fibre traits were of up to medium magnitude; but most woolly fibre traits showed no correlation with birthcoat type. The phenotypic correlation coefficients between birthcoat type and fibre traits on the other hand, indicated that all the traits, except kempy fibre traits, are uncorrelated to birthcoat type.

An analysis of fleece composition pointed out that the relative numbers and total weights of kempy and hairy fibres were positively correlated with birthcoat type, but the same traits of woolly fibres were negatively correlated with it. Furthermore, it has been observed that all the kempy and hairy fibres in Low Line comprise only about 1.5% of the total number of fibres, although all the available evidence from literature suggests that the relative number of primary follicles should be around 20%. It means that due to the effect of selection in the Low Line, about 85% of the primary follicles, in contrast to their usual behaviour of producing kemp and hair in this breed of sheep, are producing wool. The precise genetic changes underlying this alteration in the behaviour of primary follicles need further investigation. Also relevant in this connection, and associated with these changes, is the observation indicating a reduction in the weight of individual kempy and hairy fibres in the Low and High Lines respectively. As the kempy fibres are produced by primary central follicles and the hairy fibres are produced by the primary lateral follicles (Carter, 1955; Ryder, 1965), these changes in individual fibre weights seem to be due to the genetic mechanisms underlying the development of follicles.

The results of line differences in staple length and fibre length indicated that the High Line, as compared to the Low Line, has a longer staple but shorter hairy and woolly fibres. As these two fibre types are the main contributors to staple length, it would appear that hairy and woolly fibres in the High Line show fewer number of curls or crimps along their length. This is supported by the observation that the High Line hairy fibres as compared to those of the Low Line are shorter and thicker; and would thus be less prone to crimpness.

C. Commercial fleece grades

The commercial fleece quality determined by visual grading was found to be related largely to the amount of kempy and hairy fibres in the fleece and to the staple length. The length and to a lesser extent thickness of kempy fibres also appeared to affect the assessment of fleece quality. The magnitude of the differences for these traits, is high between Radnor type fleeces and Selected Welsh, Cast Welsh and Coloured fleeces, but is relatively lower within the last three fleece quality groups. The length of the staple and incidence of the kempy fibres in general, increased towards lower quality fleece groups; Cast Welsh, however, was unexpectedly found to have lower values than the Selected Welsh in both these traits.

The classification of fleeces for High and Low Lines with respect to their commercial quality (B.W.M.B. grades) indicated a constant divergence in successive years. The Low Line fleeces increased in the proportion of good quality fleeces, while a considerable increase of Coloured fleeces occurred in the High Line. As commercial fleece quality seems to rely heavily on the incidence of kempy fibres, these results are in agreement with the observation that there is a higher incidence of kempy and hairy fibres in sheep selected for hairy birthcoat type, (Type 6). At the same time increasing kempiness appears to be associated with an increase in the frequency of coloured fibres.

The prices of fleeces per pound and per hogget are negatively correlated with the selection lines. This leads to the conclusion that selection for fine birthcoat type would lead to higher economic returns from fleece sales.

SUMMARY

The data from 15 month old ewe hoggets belonging to a flock of Welsh Mountain sheep under continuous selection for birthcoat type were analysed for correlated responses in fleece and fibre traits. Mass selection based on birthcoat type had been practised within two closed breeding groups: the High Line, selected for hairy birthcoat (Type 6) and the Low Line selected for fibre birthcoat (Type 1). Selection on rams was intense, approximately 10%, but selection on females was light. This selection experiment has been in progress since 1953 at the Animal Breeding Research Organisation hill farm, Rhydyglafes, North Wales. The general farm conditions and management are fairly typical of those prevailing in the locality. Routine records for hoggets and mid-side fleece samples provided the material for this work.

The analysis of fleece measurements covered a period of 15 years (1953 to 1967) and their pooled overall mean values were as follows: fleece weight, 2.95 lb. (1877 observations), staple length, 9.76 cm. (1877 obs.) and dry wool weight per unit area of skin, 0.249 g/cm^2 (801 obs.). The annual differences between High and Low Lines (Line differences) for these traits were small but significantly correlated with the corresponding line differences in cumulated section differentials of birthcoat type. Estimates of genetic correlations of various traits with birthcoat type (observed estimates) were calculated from regression of their line differences on the line differences for birthcoat selection differential. The observed genetic correlation estimates for fleece weight, staple length and dry wool

weight were: 0.06, 0.12 and 0.12 respectively. Genetic correlation coefficients estimated by daughter-dam regression were in fairly good agreement with observed estimates; estimations by paternal half-sib analysis, however, gave negative correlation coefficients in each case.

Fleece samples from 50 unselected hoggets, for 1953 and 142 hoggets showing effects of $6\frac{1}{2}$ generations of selection for 1966, were used for analysis of fibre traits. Sub-samples of 100 - 120 fibres were separated into kempy, hairy and woolly fibres. Length, internal and external diameters, weight, medulla types and fibre densities were determined. The results indicated no significant line differences in samples for 1953 but significant differences in 1966 for all kempy fibre traits, virtually all hairy fibre traits and length and internal diameter of woolly fibres. Fleece composition line differences were significant only for 1966. The estimates for observed genetic correlations of fibre traits with birthcoat type were positive for all kempy and hairy fibre traits with the exception of length and weight of hairy fibres. In woolly fibres the only correlations with birthcoat type were in length and weight, these being positive and negative respectively.

British Wool Marketing Board (B.W.M.B.) fleece grades for High and Low Lines had shown clear differences in frequency distribution of fleece grades within lines since they were first recorded in 1958. Lines showed a consistent divergence in successive years; in 1967, good quality fleeces (Radnor types) predominated in the Low Line while a considerable increase of Low quality coloured fleeces was present in the High Line. Prices of fleece per pound and per hogget were negatively correlated with selection pressure for birthcoat type. B.W.M.B. grades were found to be related to incidence of kemp and to staple length, and in general increases in these traits lead to deterioration of commercial quality.

In general all fleece and fibre traits showed correlated responses to selection for birthcoat type. Amongst fibre types kempy and hairy fibres indicated substantial changes while woolly fibres were less affected by selection. On the basis of these findings selection for hairy birthcoat type should lead to heavier fleeces, longer staples, heavier dry wool weight per unit area of skin, higher proportions of kempy and hairy fibres, larger and heavier kempy fibres, shorter and thicker hairy fibres and shorter and lighter woolly fibres.

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